MYOLOGY OF THE LIMPKIN

By

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INTRODUCTION

The limpkin, *Aramus guarauna* (Linnaeus), is the sole living member of the avian family Aramidae of the order Gruiformes. It occurs in southeastern Georgia, Florida, the Greater Antilles, and the Neotropical mainland from Mexico to Argentina (American Ornithologists' Union, 1957). The species is known from a pre-Columbian site in Venezuela (Wetmore, 1935) and from four localities in the Upper Pleistocene of Florida (Wetmore, 1931; Brodkorb, 1956; Woolfenden, 1959). Other members of the family occur in Tertiary deposits of the Great Plains, *Aramus* sp. from the Lower Pliocene of Nebraska (Wetmore, 1928), *Aramornis longurio* Wetmore (1926b) from the Middle Miocene of Nebraska, *Gnotornis aramiellus* Wetmore (1942) from the Upper Oligocene of South Dakota, and *Badistornis aramus* Wetmore (1940) from the Middle Oligocene of South Dakota.

The living limpkin is adapted to a rather unique diet. This consists almost exclusively of large snails of the genus *Pomacea*, formerly known as *Ampullaria*, with occasional other gastropod and pelecypod mollusks (Wetmore, 1926a; Cottam, 1936). The bird usually takes the snail to a regular feeding station and with its long, specialized bill pecks through the operculum, extracts, and swallows the soft body of the mollusk.

The bird occurs primarily in grassy marshes and wooded swamps (Bent, 1926; Wetmore, 1926a; Nicholson, 1928). Where bushes or trees are available it perches and nests in them, often at some height from the ground.

Both the feeding and perching habits of the limpkin are thus quite distinctive and differ from the usual condition of its ordinal allies, the rails and cranes. Adaptations to a specialized way of life would be expected to obscure resemblances to its nearest relatives and may account for some of the disagreement over the systematic position of the Aramidae.

The subordinal position of the limpkin has not been established with certainty, although all workers have referred it to one of two suborders, the Grues or the Ralli. Some of the difficulties involved may be seen in a brief review of the opinions of other workers on the systematic position of the Aramidae. Audubon (1839) thought _Aramus_ to be allied to the rails on the basis of the viscera. Nitzsch (1867) found that the pterylosis resembles that of _Grus_ and _Psophia_ and no other bird; nevertheless, he placed it with the rails because of peculiarities of the feathers themselves. Garrod (1876) considered _Aramus_ as being closer to _Grus_, on the basis of several anatomical features, especially of the skull, sternum, and some aspects of the thigh musculature. Shufeldt (1894) placed it with the cranes but considered the species a perfect link between cranes and typical rails. Clay (1950) found the aramid Mallophaga to be rail-like and strongly

different from the type found in cranes. On the basis of the electrophoretic profiles of egg-white proteins, Sibley (1960) thought Aramus to be closer to the rails, and he mentioned the large hallux, feathered head, and color of the downy young as also being rail-like.

From a broader view, these opinions indicate that the Aramidae are definitely related to both the Gruidae and the Rallidae. A major purpose of this paper is to investigate affinities of the three families through study of their comparative myology. Fisher (1955) remarked that detailed anatomical work should solve the question of affinities.

DESCRIPTIVE MYOLOGY

During the course of this study, six limpkins were available for dissection. Two were dissected in detail and critical points were checked in the others. To represent both wading and swimming types of Rallidae, two specimens of the clapper rail, *Rallus longirostris* Boddaert, and two of the coot, *Fulica americana* Gmelin, were dissected. Some features were also examined on a specimen of the purple gallinule, *Porphyrula martinica* (Linnaeus). A specimen of the crowned crane, *Balearica pavonina* (Linnaeus), was dissected as representing a generalized gruid, and comparisons were made with Fisher and Goodman's (1955) description of the more specialized whooping crane, *Grus americana* (Linnaeus), and Berger's (1956a) study of the appendicular myology of the sandhill crane, *Grus canadensis* (Linnaeus). All dissections follow the basic plan of the excellent work by Fisher and Goodman (1955), whose descriptions are quite adequate as a guide to dissection of the species used in this study. With very few exceptions, each muscle discussed by those authors is found in each of the other species, and only a few are present that are not discussed by them.

In the descriptions of individual muscles comparisons are made on the basis of their proportions, as if all species studied were of the same size. Attention is called to

differences in general configuration, points of attachment, and function, at the specific, generic, or family levels, in an effort to determine the relationship of the limpkin to the cranes and rails.

Muscles of the Skull

1. _M_. _dermo-temporalis_

Elongate and sheet-like dermo-osseous muscle. Covers lateral surface of full length of neck. Attaches to cranium, to furculum, to _M_. _tracheohyoideus_, and to skin of neck.

Lies just beneath skin and deep to lateral edge of sheet of _M_. _constrictor colli_ in anterior half of neck. Lateral to dermal fasciculi of _Mm_. _intertransversarii_. Anterior end superficial to posterodorsal portion of _M_. _depressor mandibulae_, ventrolateral edge of cephalic part of _M_. _cucullaris_, anterodorsal portion of _M_. _rectus capitis lateralis_, side of fourth and fifth fasciculi of _M_. _rectus capitis superior_, and dorsal tip of hyoid cartilage.

Origin. In two parts, both fleshy, at opposite ends of muscle. Anterior origin from posterolateral edge of skull bordering posterior edge of temporal fossa and extending to base of opisthotic process, in a narrow line 8 mm long, just posteroventral to origins of deep slip of _M_. _adductor mandibulae externus superficialis_ and rostral slip of _M_. _adductor mandibulae externus profundus_. Anterior origin separates origins of latter two muscles from both anterior edge of origin of _M_. _depressor mandibulae_ and anteroventral edge of origin of _M_. _cucullaris_, cephalic part.

Posterior origin is in common with _M_. _tracheohyoideus_ as result of fusion of the two muscles. Common sheet originates from narrow line along anterolateral edge of ventral three-fourths of furculum, extending to mid-ventral line. From this origin the sheet runs anterodorsad onto the neck.

Insertion. By connective tissue, onto skin of neck, by all but anterior 10-18 mm of length of muscle. Fuses medially with _M_. _tracheohyoideus_ at ninth or tenth cervical vertebra to form common sheet. Posterior to fusion the common sheet covers neck, except in narrow area along middorsal and mid-ventral lines. A few short bundles, arising from furculum, leave dorsomedial edge of muscle near its posterior end and insert on skin of neck near middorsal line.

Action. Tenses skin of neck.

Comparisons. In the Gruidae the muscle undergoes change. In _Balearica_ it is similar to the condition just described in _Aramus_, but the belly is much thinner. _Grus_ is apparently unique in lacking the furcular origin and in having a very short belly. The condition of the muscle in _Grus_ might well be re-examined, since the three specimens used by Fisher and Goodman were skinned before dissection, and also because the posterior regions are very thin and difficult to see.

In the Rallidae the anterior origin differs distinctly from the condition described for _Aramus_ and the cranes by arising from the postorbital process. In _Rallus_ the posterior origin comes mainly from the anterior edge of _M_. _pectoralis_ and the anteroventral corner of the sternum, but in

Fulica it arises mainly from the sternum and sternoclavicular ligament (in Aramus it arises mainly from the furculum). In Rallus (and Aramus) the posterior origin is dorsal to the origin of M. tracheohyoideus, with the bellies of the two muscles closely fused, but in Fulica the posterior origin is ventral to the origin of M. tracheohyoideus, and the bellies are only weakly fused.

Summary. The muscle in Aramus is long and has two origins. In the cranes, Balearica agrees, but in Grus it has become extremely shortened and has lost the posterior origin. In the rails the muscle is long with both origins present, but the anterior origin lies further forward on the skull.

2. M. cucullaris, cephalic part

Moderately thin sheet. Covers posterior edge of skull and dorsolateral portion of anterior fourth of neck. Attaches to skull, to third, fourth, and fifth cervical vertebrae, and to underlying muscles.

Right and left muscles essentially fused into single sheet by continuation of fascia on superficial and deep surfaces. These fascial sheets enclose between them the paired anterior belly of M. biventer cervicis. Muscle lies deep to M. dermo-temporalis. Lateral portion contacts posterodorsal edges of third, fourth, and fifth fasciculi of M. rectus capitis superior, posterodorsal edge of M. depressor mandibulae, and anterodorsal corner of M. rectus capitis lateralis. Superficial to M. splenius capitis, M. splenius accessorius, Mm. intertransversarii between axis and fourth

cervical, and to anterior portion of M. spinalis cervicis.

Origin. By tendinous sheet from dorsolateral surface of a dorsal tubercle on diapophysis of fourth cervical vertebra and by fleshy origin from similar location on third cervical. Also originates by fleshy fibers from bony, lateral bar connecting prezygapophysis with postzygapophysis on third and fourth cervicals, by small portion arising from fifth cervical, and by fleshy fibers from Mm. intertransversari and from third, fourth, and fifth fasciculi of M. rectus capitis superior.

Insertion. Mainly by fibrous sheet, about 3 mm long, onto thin, transverse line on dorsal and lateral edges of occipital region of skull, about 1 mm dorsal to insertion of M. biventer cervicis on occipital crest. Insertion extends laterad from middorsal line, then ventrad to meet and fuse with most dorsal portion of M. depressor mandibulae. Fuses by loose fibers to dorsal edge of M. rectus capitis lateralis, to anterior regions of M. cucullaris and M. splenius capitis, and contacts dorsal edge of anterior region of origin of M. dermo-temporalis.

Action. One muscle extends head dorsolaterally, and both act together to extend head dorsally.

Comparisons. In the Gruidae the attachments in Balearica are quite similar to those of Aramus and are partly so in Grus, although Fisher and Goodman omitted some details because of obscuring fascial attachments. The fusion to M. rectus capitis lateralis and M. depressor mandibulae is

present in _Balearica_ but absent in _Grus_ because the belly is narrower.

The Rallidae agree with _Aramus_ except in attachments to adjacent muscles. In _Rallus_ the contact with _M. depressor mandibulae_ is smaller than in _Aramus_ because of partial separation by _M. rectus capitis lateralis_. In _Fulica_ the muscle contacts neither _M. rectus capitis lateralis_ nor _M. depressor mandibulae_.

Summary. The muscle attaches to _M. depressor mandibulae_ and _M. rectus capitis lateralis_ in _Aramus_, _Balearica_, and _Rallus_, but in the more specialized _Grus_ and _Fulica_ there is no contact with these muscles because the belly is narrower.

3. _M. biventer cervicis_

Very narrow and elongate, composed of two bellies connected by flattened tendon. Lies just lateral to middorsal line along all except posterior end of neck. Attaches to skull anteriorly, to fascia and to _M. spinalis cervicis_ posteriorly.

Anterior belly begins just posterior to skull and extends to about middle of third cervical. Muscle continues as tendon from middle of third cervical to middle of ninth cervical, where posterior belly begins. This belly extends to about posterior end of thirteenth cervical, where muscle again becomes tendinous. Fibrous connections join right and left muscles across mid-line at level of posterior end of thirteenth and at posterior end of fourteenth cervicals.

Right and left members lie alongside each other, separated by middorsal line, and anterior bellies fuse in cranial half. Anterior belly enclosed within fascial sheets of _M. cucullaris_, cephalic part. Most of muscle posterior to _M. cucullaris_ lies in trough along dorsomedial edge of _M. spinalis cervicis_. Connects to latter muscle only at posterior end, but is tightly held against it by strong sheet of connective tissue enclosing both. Anterior end of muscle lies superficial to _M. splenius capitis_ and to portions of _Mm. splenii colli_.

Origin. By thin tendon, entirely from dorsal surface of median portion of tendinous area of _M. spinalis cervicis_ near posterior end of fourteenth cervical.

Insertion. By short but wide aponeurosis from cranial end of anterior belly, onto thin edge of occipital crest of skull, just deep to insertion of cephalic part of _M. cucullaris_ and in contact with dorsal edge of insertion of _M. splenius capitis_. Tendon strong in most medial one-sixth, weaker laterally. Medial edge meets that of opposite muscle at middorsal line.

Action. Extends head and straightens neck.

Comparisons. In the Gruidae the posterior belly is located between the twelfth and fifteenth cervicals (between ninth and thirteenth in _Aramus_). In _Balearica_ the right and left anterior bellies are fused in less than the anterior fourth (in the anterior half in _Aramus_) and apparently are not fused at all in _Grus_. In _Balearica_ (and _Aramus_) the

anterior belly is enclosed between the fascial layers of the cephalic part of _M_. _cucullaris_, but in _Grus_ the anterior belly is completely deep to that muscle. In both cranes the tendon of origin is fused to the tendon of _M_. _spinalis cervicis_ but can be traced to an attachment on the eighteenth cervical in _Balearica_ and on the sixteenth in _Grus_ (in _Aramus_ the origin can be traced only to the tendon). In both cranes the insertion is partly fleshy and quite narrow, representing only the stronger, medial portion of the inserting tendon of _Aramus_.

In the Rallidae the posterior belly in _Rallus_ is located between the fifth and tenth cervicals, and in _Fulica_ between the seventh and eleventh. In both rallids the right and left anterior bellies are fused only at the extreme anterior end. In both rails (and in _Aramus_) the anterior belly is enclosed within the cephalic part of _M_. _cucullaris_. In both rallids the muscle arises fleshily from _M_. _spinalis cervicis_ (tendinously in _Aramus_). In both rails the insertion is much narrower and more medial than in _Aramus_.

Summary. The location of the posterior belly in the limpkin is intermediate between that of the cranes and rails, probably because of size differences. The extent of fusion between right and left anterior bellies is greatest in _Aramus_, intermediate in _Balearica_, least in the rallids, and apparently lacking in _Grus_. The wide, lateral extension of the insertion is unique in the limpkin.

4. <u>M. splenius capitis</u>

Wide and thick anterior end tapers to small posterior end, giving triangular appearance in dorsal view. Occupies most of dorsal half of extreme anterior end of neck. Attaches to skull, to axis, and to surrounding muscles.

Two muscles of pair partially connected across mid-line. Most of muscle lies deep to cephalic part of <u>M. cucullaris</u>, and small ventrolateral portion covered by <u>M. depressor mandibulae</u> and <u>M. rectus capitis lateralis</u>. Lies dorsal to region of fusion of second to fifth fasciculi of <u>M. rectus capitis superior</u>. Superficial to all of first and anterior end of second <u>Mm. interspinales</u>, and to anterior one-third of <u>M. splenius accessorius</u>.

<u>Origin</u>. Fleshy and tendinous, primarily from axis and atlas and from fascia connecting atlas to skull, with some tendinous origin from dorsal raphe of connective tissue, slightly posterior to axis. Much of origin arises from neural spine of axis, by small and tendinous anteromedial components and by mixed fleshy and tendinous components from anterolateral face of neural spine. Remainder of origin fleshy, from dorsal surface of atlas and fascia anterior to atlas, and almost contacts insertion.

<u>Insertion</u>. On all but ventromedial portion of occipital region of skull, including part of membrane closing occipital fontanelle, extending onto depression on opisthotic process. Deeper portions of insertion fleshy, with more superficial components tendinous. Bordered dorsally by insertion of

M. biventer cervicis; some fibrous connection to overlying anterior end of cephalic part of *M. cucullaris*. Partly fused laterally to underside of insertion of *M. rectus capitis* lateralis, which in turn is fused to underside of origin of *M. depressor mandibulae.* Bordered ventrolaterally by ventromedial portion of origin of *M. depressor mandibulae*, and has some fleshy insertion on posterodorsal region of belly of same portion.

Action. One muscle turns head, but two act together to extend head dorsally.

Comparisons. In the Gruidae the thickness and insertion of the muscle in *Balearica* are as in *Aramus*, but in *Grus* the belly is thinner, and the area of insertion correspondingly narrower. In *Balearica*, but not in *Grus* (or *Aramus*), a partial separation is present in the posterior end. In *Balearica* only, the muscle fuses to *M. splenius accessorius*. Only *Grus* lacks the fusion of the muscle to *M. rectus capitis lateralis*. In both cranes the muscle differs from that of *Aramus* in arising from fascia over the atlas instead of directly from the atlas and from fascia directly anterior to it. Both cranes differ from *Aramus* in lacking the portion of the origin posterior to the axis. In *Balearica* the origin from the spine of the axis is narrowly restricted to the mid-line, but in *Grus* (and *Aramus*) it is wider.

In the Rallidae the belly is thinner than in *Aramus*, especially in *Fulica*. Both rails agree with the limpkin in the connections of the muscle to adjacent ones. In both

rallids the origin from the axis is much narrower than in Aramus, being restricted to the area of the mid-line. The remainder of the origin agrees in Rallus and Aramus, but in Fulica it arises from fascia over the axis, and the portion posterior to the axis is absent.

Summary. Of the seven variations in this muscle listed above, the two cranes agree in only two points and are similar to each of the other three forms in at least as many. The two rails agree in only four, and the greatest number of similar points (six) occurs between Aramus and Rallus. Aramus has the least agreement with Balearica. The sporadic distribution of characters seems to indicate adaptability in this muscle.

5. M. splenius accessorius

Small, elongate, and flattened. Runs diagonally on dorsolateral aspect of anterior region of neck. Attaches to first three cervical vertebrae.

Although Fisher and Goodman considered this muscle as being probably related to M. splenius capitis, it may be more closely related to M. spinalis cervicis-Mm. splenius colli complex.

Anterior half deep to M. splenius capitis, and posterior half deep to M. biventer cervicis and M. cucullaris, cephalic part. Contacts dorsal edge of first of Mm. intertransversarii. Anterior portion superficial to lateral edge of first M. interspinalis and to posteromedial portion of second fasciculus of M. rectus capitis superior. Posterior

portion superficial to posterolateral part of second M. interspinalis and to tendinous insertion and part of belly of anterior end of M. spinalis cervicis-Mm. splenius colli complex.

Origin. Mixed fleshy and tendinous from anterolateral side of neural spine of third cervical, and from dorsolateral extent of postzygapophysis of axis. Origin loosely attached along posterolateral edge to adjacent anterior belly of anteriormost part of Mm. splenius colli.

Insertion. Anterior third of muscle comprised of thin, strap-like tendon which attaches to posterior process of postzygapophysis of atlas. Underside of belly has fleshy attachment to dorsolateral extent of postzygapophysis of axis, and this area of attachment considered to have functional components of both origin and insertion.

Action. Turns upper end of neck laterad.

Comparisons. In the Gruidae, Balearica has the muscle thoroughly attached to M. splenius capitis and M. spinalis cervicis, but in Grus (and Aramus) these attachments are slight or lacking. In Balearica the muscle arises and inserts on the axis in a manner more complex than in Aramus, but in Grus these attachments are absent. In Balearica the main insertion is not on the postzygapophysis of the atlas (as it is in Aramus) but is on the dorsal half of the neural arch. In Grus this is the only insertion, which Fisher and Goodman (1955) describe as being on the most ventral and lateral extent of the atlas. This origin differs remarkably from all other forms studied, unless the arch of the atlas was meant.

In the Rallidae the belly of the muscle in _Rallus_ lies between the third cervical and the axis, and passes medial to the postzygapophysis of the axis. In _Fulica_ the belly lies between the axis and atlas and passes lateral to the postzygapophysis of the axis. In both rallids the insertion onto the axis is larger than in _Aramus_, and this is the main insertion in _Rallus_. In both rallids the atlantal insertion is on a facet on the postzygapophysis instead of on a definite process as in _Aramus_.

Summary. This muscle is somewhat variable in detail, especially within the cranes and to a lesser extent between the gruids and _Aramus_. The two rails show good agreement with each other and with the limpkin. _Balearica_ resembles _Aramus_ slightly more than does _Grus_, and _Fulica_ is more like the limpkin than is _Rallus_.

6. _M. depressor mandibulae_

Short, somewhat thick, and partially separated into lateral and medial parts. Located at angle of jaw. Attaches to skull and to posterior end of mandible.

Deep, in part, to anterior end of _M. dermo-temporalis_ and to dorsal edge of _M. geniohyoideus_. _M. splenius capitis_ has part of insertion on posterolateral extent of median part, and portion of posterodorsal edge fused with _M. cucullaris_. Anteroventral edge contacts posterior end of _M. stylohyoideus_ and contacts posterior edge of superficial part of _M. pterygoideus_ ventralis on both lateral and medial sides of mandible. Anterodorsal edge of belly fused to wall

of external auditory meatus. Superficial to anterior ends of _M_. _rectus capitis lateralis_, _M_. _rectus capitis superior_ complex, and to _Ligamentum mandibulae_.

Origin. Arises from skull, mainly from region of opisthotic process. Origin and belly incompletely divided into lateral and medial parts by inserting aponeurosis of _M_. _rectus capitis lateralis_. Lateral portion composed of fleshy fibers arising from ventrolateral region of occipital crest, along posterior edge of anterior origin of _M_. _dermo-temporalis_, and these fibers fuse with aponeurosis of _M_. _rectus capitis lateralis_. Medial portion has mixed origin from posteroventral surface of opisthotic process. Anterior to separation by _M_. _rectus capitis lateralis_, two portions join with fleshy origin from all but lateral surface of opisthotic process, with strong tendon from anterior edge of opisthotic process, and with tendinous fibers from ventrolateral edge of basitemporal plate. Lateral and medial portions of muscle remain partially separable through middle of belly.

Insertion. Fleshy, except for tough, superficial fascial sheet. Attaches to most of posterior face of mandible.

Action. Opens mouth by depressing mandible.

Comparisons. In the Gruidae the muscle differs from that of _Aramus_ in contributing to the origin of _M_. _dermo-temporalis_ and in having much less connection to _M_. _rectus capitis lateralis_. In _Balearica_ the origin extends to the dorsal edge of the occipital region of the skull, and the belly is slightly fused to the insertion of _M_. _splenius_

capitis. In *Grus* (and *Aramus*) the origin does not extend so far dorsad, and it does not connect to the insertion of *M*. *splenius capitis*. *Balearica* resembles *Aramus* but differs from *Grus* in having part of the origin from the basitemporal plate.

In the Rallidae the muscle in *Rallus* is divided into anterodorsal and posteroventral portions, unlike the division into lateral and medial portions in *Fulica* (and *Aramus*). In both rallids the muscle resembles that of *Aramus* in not contributing to the origin of *M*. *dermo-temporalis* or fusing to the insertion of *M*. *splenius capitis*. Both rallids differ from *Aramus* in having part of the origin from the basitemporal plate and in having no fusion of the muscle to the cephalic part of *M*. *cucullaris*.

Summary. Only minor variations are present, and points of comparison indicate that *Aramus* has similarities to both cranes and rails.

7. *M*. *rectus capitis lateralis*

Thick, fleshy, horizontally oriented sheet at posterior end tapers to much narrower, vertically oriented aponeurosis at anterior end; runs from posteroventral to anterodorsal locations. Lies on side of anterior end of neck. Attaches to second, third, and fourth cervicals and to skull.

Anterodorsal end lies partly deep to anterior portion of *M*. *dermo-temporalis*, to ventrolateral corner of insertion of cephalic part of *M*. *cucullaris*, and to a posterodorsal portion of lateral part of *M*. *depressor mandibulae*.

Posteroventral end partly covered by anterior end of _M_. _flexor colli brevis_. A short length of dorsal edge is fused to ventral edge of cephalic part of _M_. _cucullaris_ near anterior ends of the two muscles. Ventral side of belly very loosely connected to dorsal side of _M_. _rectus capitis ventralis_. Posterior portion contacts _M_. _flexor colli profundus_. At anterior end muscle lies superficial to ventrolateral edge of origin of _M_. _splenius capitis_ and to posterodorsal extent of medial origin of _M_. _depressor mandibulae_. Middle of belly superficial to portions of last three fasciculi of _M_. _rectus capitis superior_.

Origin. Arises by fleshy and tendinous fibers from ventrolateral edges of hypopophyses of second, third, and fourth cervicals. At extreme posterior end has some fleshy fusion to _M_. _rectus capitis ventralis_, and origins of two are contiguous.

Insertion. By thin aponeurosis, mostly in common with lateral part of _M_. _depressor mandibulae_, onto narrow line on ventrolateral portion of occipital crest and extending onto posterolateral edge of opisthotic process. Most of attachment lies adjacent to posterior edge of anterior origin of _M_. _dermo-temporalis_. Insertion separates origin of _M_. _depressor mandibulae_ into lateral and medial parts. Dorsal tip of insertion lies deep to ventrolateral edge of cephalic part of _M_. _cucullaris_, near its insertion, and anterior half of dorsal border loosely joined by connective tissue to latter muscle, although bellies not in contact.

Action. One muscle acts to turn head laterad, and both together extend (beugung of Gadow, 1893) head on neck.

Comparisons. In the Gruidae the attachment in Balearica to M. rectus capitis lateralis is as in Aramus, except for being weaker. In Grus a strong attachment exists between these two muscles, but only on the left side. The asymmetry is apparently correlated with the position of the trachea. Both cranes differ from Aramus in having none of the muscle deep to or fused with the cephalic part of M. cucullaris and none superficial to M. depressor mandibulae. In Balearica the origin from the second through the fifth cervicals, but in Grus only from the third and fourth cervicals (in Aramus it arises from the second through the fourth). In Balearica the insertion is as in Aramus, attaching to a long line by a thin, wide aponeurosis, but in Grus a thickly rounded tendon inserts on a small oval facet. Both gruids differ from Aramus in lacking a common insertion with M. depressor mandibulae.

In the Rallidae the connection to M. rectus capitis ventralis is symmetrical, but it is stronger in Fulica. In both rallids then fusion to M. cucullaris and the connection to M. depressor mandibulae are stronger than in Aramus.

Summary. Variations among the three families are slight. Minor characteristics of Aramus agree well in Balearica, but poorly in Grus. The Rallidae are rather constant and agree well with Aramus.

8. _M_. _rectus_ _capitis_ _superior_

Relatively thick and composed of five fasciculi, appearing in lateral view as an elongate triangle with apex at posterior end. Located on side of upper neck. Attaches to first five cervicals, to skull, and to parts of _M_. _flexor_ _colli_ _brevis_ and _M_. _flexor_ _colli_ _profundus_.

First four fasciculi diverge from small, common anterior end, but fifth largely independent. Each successive fasciculus attaches to cervical vertebra of corresponding numbers, although third and fifth have additional attachments. Successive fasciculi, therefore, of increasing thickness and length from anterior to posterior ends. Separations between last three fasciculi indistinct in one specimen.

Fourth fasciculus partly superficial to fifth, and some fleshy connection exists between them. Much of muscle complex lies deep to _M_. _rectus_ _capitis_ _lateralis_. Most of dorsal edge of complex adjoins first five _Mm_. _intertransversarii_ and ventrolateral edge of cephalic part of _M_. _cucullaris_. More posterior portions dorsal to posterior portions of _M_. _rectus_ _capitis_ _lateralis_ and _M_. _flexor_ _colli_ _brevis_. Superficial to all but posterior end of _M_. _flexor_ _colli_ _brevis_, to anterior end of _M_. _longus_ _colli_, and to anterior end of _M_. _flexor_ _colli_ _profundus_.

Origin. First fasciculus arises fleshily from side of atlas, between dorsolateral border of condylar facet and insertion of _M_. _splenius_ _accessorius_ on posterior process of postzygapophysis. Second fasciculus originates fleshily and

tendinously from side of axis, along bony ridge extending from prezygapophysis to postzygapophysis. Third fasciculus has fleshy and tendinous origin, similar to that of second, from lateral bar of third cervical, but has additional fleshy origins from fused rib of third cervical and from centrum of second cerfical. Fourth fasciculus also has mixed origin from whole length of lateral bar of fourth cervical and from fused rib of same vertebra. Fifth fasciculus arises fleshily from side of axis and from large areas on fused ribs of third and fourth cervicals, alongside origins of previous two fasciculi. Fifth fasciculus arises also from lateral bars of third and fourth cervicals and from side of prezygapophysis of fifth cervical. Small, deep slip arises in common with main part of fifth fasciculus and with M. flexor colli brevis. All fasciculi but first have some of origin in contact with adjacent portions of Mm. intertransversarii, and all but first and second fasciculi have origins connected to ventrolateral portions of origin of cephalic part of M. cucullaris. Fifth fasciculus loosely connected at posterior end to M. flexor colli brevis.

Insertion. Fasciculi one through four have common insertion, by small tendon, onto triangular area on posterolateral region of basitemporal plate; this surface of attachment faces posteroventrally. Fifth fasciculus has independent tendinous insertion on posteriorly directed process from ventrolateral part of atlas, small attachment to hypapophysis of axis, and small deep slip that passes separately to attach to first fasciculus of M. flexor colli

profundus, which inserts on pleurapophysis of axis.

Action. One muscle turns head and upper neck ventrolaterad, but both muscles together bend head and upper neck ventrad.

Comparisons. In the Gruidae *Balearica* is unique in having the third fasciculus divided into two parts. In *Balearica* the origins for fasciculi three, four, and five are on a ligament alongside the centra of the vertebrae involved (this ligament is ossified in *Aramus*), but in *Grus* the ligament is apparently absent, and the fasciculi arise from the centrum. *Balearica* agrees with *Aramus* in having several origins for each of these three fasciculi, but *Grus* has few. In *Balearica* the deep slip of the fifth fasciculus is divided into outer and inner parts, but only one exists in *Grus* (and *Aramus*). The inner part in *Balearica* inserts independently and seems to correspond to the single slip of the others; the outer part inserts with the main fifth fasciculus, from which it is apparently derived. In *Balearica* and *Grus* the main insertion is partly on fascia connecting to the skull (directly to the skull in *Aramus*). The muscle in *Grus* is unique in having a common insertion with *M. flexor colli brevis*.

In the Rallidae the origins of fasciculi three, four, and five have fewer attachments, especially to pleurapophyses, than in *Aramus*. In *Rallus* the fifth fasciculus is short and is completely deep to the third and fourth, but at least part of the fifth is exposed in *Fulica* (largely exposed in

Aramus). In *Rallus* the fifth fasciculus has no origin from the fifth cervical, but some of the origin arises from that vertebra in *Fulica* (and *Aramus*). The fifth fasciculus in the rallids lacks the deep slip found in *Aramus*. In *Rallus* the fifth fasciculus inserts independently as in *Aramus*, but a common insertion with *M. flexor colli brevis* exists in *Fulica*. Individual variation was found in one specimen of *Rallus*, in which the third and fourth fasciculi were inseparably fused on one side.

Summary. The inconstancy of the muscle indicates adaptability. The Rallidae are unique in lacking the deep slip of the fifth fasciculus. Evidences of additional separation (in *Balearica*) and fusion (in *Rallus*) of fasciculi indicate that these slips probably evolved from a single, larger muscle, and rearrangement is still occurring.

9. *M. rectus capitis ventralis*

Elongately triangular, with slightly wider anterior end tapering uniformly to pointed posterior end; composed of lateral and medial parts. Located on ventral side of neck in region of throat. Attaches to first five cervicals, to connective tissue in mid-line, loosely to surrounding muscles, and to skull.

Lateral part has irregular, transverse partition of connective tissue in middle of belly, causing muscle to appear to be formed by fusion of ends of two shorter muscles. Medial part composed of loosely connected bundles.

Lateral part longer and partly superficial to medial part. Right and left lateral parts loosely connected posterior to medial part. Right and left medial parts in contact throughout length at mid-ventral line, strongly fused at anterior ends. Lateral and medial parts mostly very loosely connected, but somewhat fused near insertions. Muscle lies just dorsal to esophagus, with portion of posterior end deep to _M_. _longus_ _colli_. Lateral side of muscle contacts medial side of _M_. _rectus_ _capitis_ _lateralis_ and _M_. _longus_ _colli_, and posterior end of each part contacts _M_. _rectus_ _capitis_ _superior_. Medial part contacts an anterior portion of insertion of _M_. _flexor_ _colli_ _profundus_.

Origin. Lateral part arises fleshily from ventral face of hypapophysis of fourth cervical, ventral surface of centrum of fifth cervical, and from connective tissue around carotid artery ventral to sixth cervical. Medial part takes fleshy and tendinous origin from narrow area along mid-ventral line, including hypapophyses and fascia between hypapophyses, of first four cervical vertebrae. Lateral part has some connection to _M_. _longus_ _colli_ at posterior end. Origin of medial part loosely connected to medial side of origin of _M_. _rectus_ _capitis_ _lateralis_, to an anterior portion of insertion of _M_. _flexor_ _colli_ _profundus_, and appears to be continuous with its own insertion on skull.

Insertion. Lateral part inserts by narrow, rounded tendon onto small tubercle (probably same as occipital process of Fisher and Goodman, 1955) on posterolateral area of

basitemporal plate. Medial part inserts fleshily on larger area, including nearly all of ventral surface of basitemporal plate. Lateral and medial parts somewhat fused near origin.

Action. Flexes head on neck.

Comparisons. In the Gruidae the muscle is symmetrical in *Balearica* (and *Aramus*) but is asymmetrical in *Grus*. The transverse partition in *Aramus* is lacking in both gruids. *Balearica* resembles *Aramus* in having the two lateral parts only weakly connected. In *Grus* the right and left medial parts are inseparably fused, and the two lateral parts are much more closely connected than in *Balearica* (or *Aramus*). In *Balearica* the attachment to *M. rectus capitis lateralis* is symmetrical and slightly stronger than in *Aramus*, but in *Grus* it is much stronger on the left side and absent on the right. In *Balearica* (and *Aramus*) the lateral part originates bilaterally from the fourth and fifth cervicals and connective tissue below the sixth. In *Grus* the right lateral part arises from the fourth and sometimes the fifth cervicals, but the left one arises from the fourth, fifth, and sometimes the sixth cervicals. In *Balearica* (and *Aramus*) the origin of the medial part is from the skull to the fourth cervical. In *Grus* the left medial part agrees, but the right only extends posteriad to the third cervical. In *Balearica* (and *Aramus*) the insertion of the lateral part is located further posterior than in *Grus*. This attachment is elongate in *Balearica* and oval in *Grus* (rounded in *Aramus*).

In the Rallidae the muscle is symmetrical in Rallus, but the right lateral part is sometimes longer in Fulica (this asymmetry is opposite to that of Grus). Neither rallid has the transverse partition of Aramus. In Rallus the posterior extent of the lateral part reaches the connective tissue ventral to the sixth cervical, but only reaches to the region of the fifth cervical in Fulica.

Summary. Minor features are inconsistent within the cranes, consistent within the rallids, with better agreement with Aramus. The limpkin agrees best with Balearica in the cranes and with Rallus in the rails. The inconsistency within the gruids is apparently a consequence of the specializations in Grus, involving asymmetry and coiling of the trachea. Slight asymmetry sometimes occurs in Fulica, but it is opposite to that of Grus.

10. M. flexor colli brevis

Elongately triangular, with apex at posterior end; obliquely divided into four separate fasciculi. Located on lateral portion of upper neck. Attaches onto second through seventh cervicals, to M. longus colli, to Mm. intertransversarii, and loosely to M. rectus capitis superior.

Anterior half located deep to M. rectus capitis superior, and edges of posterior portion partly deep to Mm. intertransversarii. Partly in common with anterior end of M. longus colli. Ventral portions contact origins of M. rectus capitis lateralis. Superficial to most of M. flexor colli profundus and portions of Mm. intertransversarii.

Origin. First and most anterior fasciculus originates fleshily from lateral surface of centrum of third cervical and fleshily from lateral bar of fourth cervical. Second fasciculus takes fleshy origin from prezygapophysis and lateral surface of centrum of fifth cervical. Third fasciculus arises from postzygapophysis of fifth cervical. Fourth fasciculus has origin from pleurapophysis of sixth and anterolateral corner of prezygapophysis of seventh cervical. Three posterior parts loosely connected to *Mm. intertransversarii*.

Insertion. First fasciculus inserts partly along posterior edge of pleurapophysis of third cervical and remainder fuses with fifth fasciculus of *M. rectus capitis superior*. Second fasciculus inserts on pleurapophysis of third cervical in common with portions of *M. longus colli*. Third fasciculus inserts on distal tip of pleurapophysis of fourth cervical. Fourth fasciculus inserts on pleurapophysis of fifth cervical and sometimes on distal end of pleurapophysis of fourth cervical.

Action. One muscle bends upper neck ventrolaterad, but both together turn upper neck ventrad.

Comparisons. In the Gruidae *Balearica* has the muscle divided into fasciculi as in *Aramus*. Divisions are apparently similar in *Grus*, but Fisher and Goodman (1955) did not list them in detail. In *Grus* a portion of the most anterior fasciculus arises from the axis and the third cervical and inserts on the fifth fasciculus of *M. rectus capitis superior*,

but this fasciculus is an inseparable part of M. rectus capitis superior in Balearica (and Aramus). The anterior portion of the muscle has apparently changed its associations. This supports the idea of Fisher and Goodman (1955) that M. flexor colli brevis could be considered as slips of the M. rectus capitis superior complex. The second and third fasciculi in Balearica (and Aramus) apparently represent divisions of a single fasciculus arising from the fifth cervical in Grus. Both cranes disagree with Aramus in having a portion originating from the pleurapophysis of the fifth cervical. In Balearica (and Aramus) the origin has components, not present in Grus, from the fourth and seventh cervicals.

In the Rallidae the muscle is divided as it is in Aramus. Both rallids differ from Aramus in possessing, as part of M. flexor colli brevis, the portion that arises from the atlas and third cervical and attaches to the fifth fasciculus of M. rectus capitis superior. In Rallus only, a small portion arises from the fifth cervical. In Fulica (and Aramus) portions arise from the fourth and seventh cervicals, but in Rallus the origin from the seventh is lacking.

Summary. The major features of this muscle are fundamentally similar but show considerable variation in the arrangement of the parts among the three families, as well as within the Gruidae and the Rallidae. In some small details of attachment there is greater similarity between Aramus and Balearica than between Balearica and Grus. Intrafamilial

variation, along with distinct interfamilial similarity, indicates that this muscle has been variously specialized in different genera.

11. M. flexor colli profundus

A disjunct series of six fasciculi connecting anterior vertebrae. Located on ventrolateral side of upper neck. Attaches to first six cervicals, to M. longus colli, and to M. rectus capitis superior.

Most of muscle lies deep to M. flexor colli brevis, and small middle portion deep to M. rectus capitis superior. Posterior end deep to M. longus colli, and third fasciculus deep to one of Mm. intertransversarii. Ventral extent in contact with medial part of M. rectus capitis ventralis and posterior portion of M. rectus capitis lateralis.

Origin. First two fasciculi closely connected. First fasciculus arises from anteroventral edge of pleurapophysis of third cervical. Second fasciculus arises from medial side of pleurapophysis and anteroventral corner of centrum of third cervical. Third fasciculus has fleshy and tendinous origin from anteromedial edge of pleurapophysis of fourth cervical, from lateral part of centrum and hypapophysis of third cervical, and loosely from medial side of pleurapophysis of third cervical. Fourth fasciculus arises fleshily or by strong, narrow tendon from anterior face of prezygapophysis of fifth cervical and fleshily from lateral side of centrum and medial side of pleurapophysis of fourth cervical. Fifth fasciculus has mostly fleshy origin from anterior

corner of ventrolateral portion of sixth cervical and fleshy origin from ventrolateral edge of full length of centrum of fifth cervical. Sixth fasciculus arises, mostly tendinously, from sixth cervical, just ventral to and in contact with origin of fifth fasciculus pnd partly in common with origin of one of fasciculi of M. longus colli.

Insertion. First fasciculus receives medial slip of fifth fasciculus of M. rectus capitis superior and inserts tendinously on pleurapophysis of axis. Second fasciculus inserts fleshily on most of lateral face of hypapophysis of axis and on ventral extent of atlas. Third fasciculus has mixed insertion along ventrolateral edge of hypapophysis of axis. Fourth fasciculus has fleshy insertion onto posterolateral portion of hypapophysis of third cervical. Fifth fasciculus inserts on posterior corner of ventrolateral region of centrum of fourth cervical. Sixth fasciculus has fleshy insertion onto ventrolateral edge of full length of centrum of fifth cervical but may also insert with fifth fasciculus on fourth cervical. Insertions of third and fourth fasciculi contact origin of M. rectus capitis lateralis. Insertion of fifth fasciculus contacts origin of medial part of M. rectus capitis ventralis and part of insertion of M. longus colli.

Action. Contraction of muscle on one side bends upper neck in ventrolateral direction, but both sides together bend upper neck in ventral direction.

Comparisons. In the Gruidae, Balearica agrees with Aramus in having the first two fasciculi fused, but in Grus

they are separate. In <u>Balearica</u> the fifth and sixth fasciculus each have a connection to a portion of <u>M</u>. <u>longus colli</u>, but in <u>Grus</u> only the fifth is so connected (neither connection exists in <u>Aramus</u>). The third fasciculus in <u>Balearica</u> originates from the centrum, but not from the hypapophysis or pleurapophysis of the third cervical; all three origins are present in <u>Grus</u> (and <u>Aramus</u>). In <u>Balearica</u> (and <u>Aramus</u>) the fourth fasciculus arises partly from the pleurapophysis of the fourth cervical, but this origin is not found in <u>Grus</u>. In <u>Balearica</u> the third fasciculus has an additional deep portion that inserts on the whole lateral face of the hypapophysis of the third cervical, but in <u>Grus</u> (as in <u>Aramus</u>) this portion is not present, and the insertion of the third fasciculus is only on the axis.

In the Rallidae the first two fasciculi differ from the ones in <u>Aramus</u> in being separate. In <u>Rallus</u> the third fasciculus has a connection to <u>M</u>. <u>longus colli</u>, not present in <u>Fulica</u> (or <u>Aramus</u>). The fifth and sixth fasciculi are separate in <u>Rallus</u> (and <u>Aramus</u>), but they are strongly connected in <u>Fulica</u>. In <u>Rallus</u> (as in <u>Aramus</u>) the insertions of the first and second fasciculi occupy nearly all of the lateral face of the hypapophysis of the axis, but these insertions occupy only very small areas in <u>Fulica</u>. In <u>Rallus</u> the fifth fasciculus is large and inserts partly on the third cervical, whereas this part is smaller and has no insertion on the third cervical in <u>Fulica</u> (or <u>Aramus</u>).

<u>Summary</u>. The variations in this muscle among the genera are slight, but inconsistent within the Gruidae and Rallidae.

The divergences primarily involve small variations in fascicular attachments of the various parts.

12. M. adductor mandibulae externus superficialis

Wide and flat in posterior third; narrow and somewhat thickened in anterior two-thirds. Runs longitudinally along lateral portion of skull. Attaches to temporal fossa, to mandible, to M. depressor mandibulae, and to deeper adductor muscles.

Bridged over by postorbital ligament and jugal bar of skull. Ventral edge of posterior half closely attached to dorsal edge of rostral slip of M. adductor mandibulae externus profundus, fused to anterior side of posterodorsal extent of M. depressor mandibulae and contacts anterior origin of M. dermo-temporalis. Superficial to M. adductor mandibulae externus medialis and M. adductor mandibulae medius.

Origin. Arises fleshily from posterior two-thirds of temporal fossa, and also by ossified tendon continuous with bone of ventral portion of temporal fossa. Ventral edge of origin arises from tendon of origin of M. adductor mandibulae medius.

Insertion. Two separate insertions. One mainly fleshy, on superficial fascia and ossified tendon of most lateral part of M. adductor mandibulae medius, with superficial fascia extending farther to insert directly on bone of mandible along anterodorsal edge of latter muscle. Other part of

insertion attaches onto coronoid process of mandible, by very strong tendon partly in common with insertion of _M. adductor mandibulae externus medialis_.

Action. Closes mouth by adducting mandible.

Comparisons. In the Gruidae the muscle in _Balearica_ is undivided as in _Aramus_, but in _Grus_ it is composed of separate superficial and deep parts. In _Balearica_ the muscle is separated from _M. depressor mandibulae_, but it has intimate contact with the anterior origin of _M. dermo-temporalis_. _Grus_ agrees with _Aramus_ in having the muscle contact _M. depressor mandibulae_, but in neither is there close contact with _M. dermo-temporalis_. In _Balearica_ a narrow, ossified tendon originates from the ventral portion of the temporal fossa in common with _M. adductor mandibulae medius_ (the tendon is similar but separate in _Aramus_). This tendon corresponds to the independent, unossified, main origin of the superficial part in _Grus_, and the remainder of the origin of the superficial part in _Grus_ is from fascia of the deep part. The other origin in _Balearica_ (and _Aramus_) arises fleshily from most of the temporal fossa and corresponds to the fleshy origin of the deep part from the dorsoposterior region of the temporal fossa in _Grus_. In both cranes the most anterior insertion is by a strong tendon (unlike the weak and superficial fascia attachment in _Aramus_) on the dorsolateral edge of the mandible. This is the insertion of only the superficial part in _Grus_. In _Balearica_, but not in _Grus_, there is a small area (large in _Aramus_) of fleshy attachment to

M. adductor mandibulae medius, just posterior to the previous tendon. The deeper and more posterior insertion on the coronoid process of the mandible is similar in both cranes and agrees with Aramus, but this is the insertion of only the deep part in Grus.

In the Rallidae the muscle is divided in the posterior region into two heads that seem generally equivalent to the superficial and deep parts in Grus. Fulica is unique in having some of the deep head superficial to the superficial head, and in showing individual variation in the size of the muscle, so that it is sometimes superficial to part of M. adductor mandibulae externus profundus. In both rallids the muscle has more extensive contact with M. depressor mandibulae than in the limpkin, and the posterior portion is overlapped by M. dermo-temporalis (not overlapped in Aramus). In Rallus alone, this origin is enclosed by superficial fascia, by which it is attached to the deep head. The deeper origin in both rallids is about the same as that of Aramus. In both Rallus and Fulica (but not in Aramus) each of the two heads arises partly from M. adductor mandibulae externus medialis. In both rallids the two heads fuse before inserting. The most anterior attachment is similar to the corresponding attachment in Aramus, except that it is located more posteriorly and lacks attachment to M. adductor mandibulae medius.

Summary. The muscle apparently has undergone several small-scale modifications in the various genera. It is composed of only one part in Aramus and Balearica, but it is

composed of two parts in _Grus_ and is partly divided in the rallids. The most distinctive feature is the small, tendinous origin of the superficial part in Aramidae and Gruidae, contrasted with the wide and fleshy attachment of the corresponding origin in Rallidae. In other more minor features _Aramus_ has more similarity with gruids than with rallids.

13. _M. adductor mandibulae externus profundus_

Small, elongate muscle composed of rostral and caudal parts; rostral part superficial with bipinnate belly. Posterior end of muscle lies just posterior to ear opening. Anterior end passes beneath postorbital ligament and beneath posterior end of jugal bar. Attaches to temporal fossa, quadrate, mandible, and to tendon of origin of lateral part of _M. adductor mandibulae medius_.

Anterior end partly deep to lateral part of _M. adductor mandibulae medius_. Posterior end in contact with ventral edge of _M. adductor mandibulae externus superficialis_ and with anterior origin of _M. dermo-temporalis_. Middle of belly attaches to ventral side of tendon of origin of lateral part of _M. adductor mandibulae medius_. Superficial to most of medial part and some of origin of lateral part of _M. adductor mandibulae medius_.

Origin. Rostral part arises, partly fleshily and partly by ossified tendon, from ventral region of temporal fossa, fleshily from lateral surface of quadrate, and by ossified tendon from otic process of quadrate. Dorsal edge of origin

arises from tendon of origin of *M. adductor mandibulae medius*. Caudal part arises fleshily from lateral surface of main body of quadrate and from proximal part of orbital process of quadrate, in common with portion of origin of rostral part.

Insertion. Rostral part has mixed insertion, partly by ossified tendon and partly by fleshy fibers, onto dorsolateral edge of mandible. This attachment partly deep to, and partly posterior to, insertion of lateral part of *M. adductor mandibulae medius*, to which there is some connection. Caudal part inserts partly fleshily and partly by ossified tendon, attaching strongly onto dorsal edge of mandible at level of small foramen in angular bone.

Action. Closes mouth by adducting mandible.

Comparisons. In the Gruidae the muscle in *Balearica* is divided, but the superficial part is small and seems to correspond to the upper, tendinous portion of the rostral part in *Grus* (and *Aramus*). The deeper part in *Balearica* includes portions corresponding to all the caudal part as well as to the deeper and more ventral portions of the rostral part of *Grus* (and *Aramus*). This muscle in *Balearica* is neither connected to nor covered by *M. adductor mandibulae medius* (connected but not covered in *Aramus*). In *Grus* the dorsal end of the caudal part is fused to the medial slip of the previous muscle, and the anteroventral portion of the rostral part is covered by the lateral part of the same muscle. In *Grus*, but not *Balearica* (or *Aramus*), the dorsal end of the rostral part is covered by the deep slip of *M. adductor mandibulae externus superficialis*.

In the Rallidae the muscle is slightly smaller than in Aramus. In Rallus the rostral and caudal parts are entirely fused, and in Fulica they are separate only at their insertions (fused only at origins in Aramus). Fulica shows individual variation in sometimes having the dorsal edge of the rostral part deep to M. adductor mandibulae externus superficialis, because of variation in the size of the latter muscle. In Rallus and Fulica (but not in Aramus) the origin of the rostral part includes portions from the orbital cranium, just medial to the postorbital process.

Summary. Balearica appears somewhat specialized in having the two parts separated in a different plane from that of Grus and the non-gruids. In other minor features the rallids are different from the non-rallids in having the muscle smaller and in having the two parts mostly fused, although a small amount of similar fusion occurs in Aramus. The two rallids are also distinct from the other two families in having the origin extending into the orbit.

14. M. adductor mandibulae medius

Composed of thin and somewhat spatulate lateral part and thicker medial part. Located below eye; lateral part one of most superficial adductors of jaw, medial part deepest adductor of jaw. Attaches to temporal fossa, to quadrate, to mandible, and to inserting tendon of M. adductor mandibulae externus medialis.

Bridged by postorbital ligament and jugal bar. Tendon of origin of lateral part deep to adjacent edges of

M. adductor mandibulae externus superficialis and rostral part of M. adductor mandibulae externus profundus, where these two muscles adjoin. Dorsal half of anterior end deep to and fused with M. adductor mandibulae externus superficialis. Medial part deep to all other adductors of jaw. Most ventral extent of lateral part contacts superficial part of M. pterygoideus ventralis. Posterior end of lateral part superficial to portion of caudal part of M. adductor mandibulae externus profundus. Anterior end of lateral part superficial to anterior end of rostral part of M. adductor mandibulae externus profundus and to most posterior insertion of M. adductor mandibulae externus superficialis.

Origin. Lateral part arises by slender, ossified tendon from anteroventral extent of temporal fossa. This tendon also furnishes part of dorsal edge of origin of rostral part of M. adductor mandibulae externus profundus and ventral edge of origin of M. adductor mandibulae externus superficialis. Muscle narrow in proximal third, then belly and an enclosed ossified tendon flare to become wide and fleshy in anterior two-thirds. Medial part has mixed origin from anterior edge of body and anterior and anteromedial edges of orbital process of quadrate.

Insertion. Lateral part inserts fleshily over region about 23 mm long, including mandibular foramen. Posterior edge of insertion on anterior end of rostral part of M. adductor mandibulae externus profundus, and M. adductor mandibulae externus superficialis shares dorsal part of insertion. Medial part inserts narrowly on posterolateral edge

of mandible just anterior to quadrate and extensively onto large depression on medial side of mandible. Covers area from internal articular process to posterior third of mandibular foramen. Tendon of *M. pseudotemporalis* passes through medial part, which it partially divides along superficial side. Tendon of *M. adductor mandibulae externus medialis* inserts on anterodorsal edge of medial part.

Action. Closes mouth by adducting mandible.

Comparisons. In the Gruidae the muscle in *Balearica* differs from that of *Aramus* in lacking contact with *M. pterygoideus ventralis*, but the contact sometimes exists in *Grus*. In *Balearica* the lateral part is unique in having a large ossified tendon of origin in addition to the smaller ossified tendon like that of *Grus* (and *Aramus*) and in having a dense fascial sheet that covers the lateral edge of the medial part and fuses with the inserting tendon of *M. pseudotemporalis*. *Balearica* (like *Aramus*) has no origin of this muscle from the lateral face of the quadrate, but that area furnishes a portion of the origin of the medial part in *Grus*.

In the Rallidae the proximal end of the lateral part is located farther dorsally and is deep only to *M. adductor mandibulae externus superficialis* (in *Aramus* this portion is deep to the latter muscle as well as to *M. adductor mandibulae externus profundus*, since it lies beneath the line of junction between them). The two rallids have only the dorsal edge of the lateral part deep to the anterior end of *M. adductor mandibulae externus superficialis* and have no insertion

of that muscle on the lateral part (in _Aramus_ most of the dorsal half of the lateral part lies deep to _M_. _adductor mandibulae externus superficialis_ and furnishes a wide area of insertion for it). The rallids differ from _Aramus_ in having the tendinous portion of the origin of the lateral part unossified.

Summary. In _Aramus_ the muscle agrees somewhat better with that of _Grus_ than _Balearica_, but the variations are mostly minor. The most distinctive characters are the extra tendon of origin of the lateral part and the dense, lateral fascia in _Balearica_, but these apparently are specializations, since they are not found in _Grus_ or _Aramus_. The differences between the limpkin and the Rallidae are similarly minor, and the two rallids agree closely, even in small details.

15. _M. adductor mandibulae externus medialis_

Small and elongate muscle. Deepest of adductors in temporal fossa; located just ventral to orbit. Attaches to temporal fossa, to _M_. _adductor mandibulae externus superficialis_, and indirectly to mandible.

All but anterodorsal edge of muscle deep to anterodorsal edge of middle of belly of _M_. _adductor mandibulae externus superficialis_. Superficial to belly of _M_. _pseudotemporalis bulbi_ and to posterodorsal part of origin of _M_. _pesudotemporalis_.

Origin. Arises partly fleshily and partly by ossified tendon arising as continuation of bone of temporal fossa.

Origin covers small area in anterodorsal region of temporal fossa, just posterior to posterodorsal part of origin of *M. pseudotemporalis*.

Insertion. Belly attaches to ossified tendon of *M. adductor mandibulae externus superficialis* and inserts in common with it on coronoid process of mandible and on anterodorsal edge of medial part of *M. adductor mandibulae medius*. Muscle therefore inserts indirectly on mandible.

Action. Aids in closing mouth by adducting mandible.

Comparisons. In the Gruidae, *Balearica* has the origin larger and more completely aponeurotic than in *Grus* (or *Aramus*). In *Balearica* the side of the muscle is completely fused to the inner side of *M. adductor mandibulae externus superficialis*, and the insertion is on the same muscle (the small insertion is the only attachment to that muscle in *Aramus*). In *Grus* there is no attachment to *M. adductor mandibulae externus superficialis*, and the insertion is entirely on *M. adductor mandibulae medius*.

In the Rallidae the belly of the muscle in *Rallus* lies between the two parts of *M. adductor mandibulae medius*, but does not in *Fulica* (or *Aramus*). In *Rallus*, but not in *Fulica* (or *Aramus*), there is fusion to the dorsal edge of the rostral part of *M. adductor mandibulae externus profundus*. In both rallids (and in *Aramus*) the insertion is on *M. adductor mandibulae externus superficialis*. In *Rallus* only, there is an additional, more direct connection to the mandible.

Summary. This muscle in *Aramus* has some differences from the corresponding muscle in both *Balearica* and

Grus, and some differences are found between the two cranes. The insertion on M. adductor mandibulae medius is similar in Balearica and Aramus, but in Grus it is on a different muscle. The muscle shows some minor differences between the two rallids, but in Fulica and Aramus the muscle agrees well.

16. M. pseudotemporalis

Rather pyramidal muscle with flat planes of anterior and lateral faces oriented at right angles to each other; distal third comprised entirely of narrow, ossified tendon. Located in anterior region of temporal fossa, posterior and ventral to postorbital process, and in orbit, medial to postorbital process. Attaches to temporal fossa, orbit, and to mandible.

Portion of origin from temporal fossa deep to M. adductor mandibulae externus medialis and to posterior end of M. adductor mandibulae externus superficialis, although very small portion of dorsal edge visible dorsal to latter muscle in some specimens. Much of lateral face of muscle deep to belly of M. pseudotemporalis bulbi. Distal end of muscle deep to belly of M. adductor mandibulae externus superficialis and to tendinous insertion of rostral part of M. adductor mandibulae externus profundus. Tendon of insertion partly superficial to, and partly enclosed by, medial part of M. adductor mandibulae medius.

Origin. Arises fleshily from anterodorsal corner of temporal fossa, from medial surface of postorbital process, and from area occupying about one-fourth of posterior wall of orbit, just medial to postorbital process. Proximal end of

muscle covered by strong superficial fascia which adds tendinous component to origin.

Insertion. Ossified tendon forms within belly near proximal end of muscle and extends anteroventrad to become sole insertion, attaching to medial aide of mandible onto tubercle in posterior part of depression for insertion of M. adductor mandibulae medius.

Action. Aids in closing mouth by adducting mandible.

Comparisons. In the Gruidae the origin from the temporal fossa in Balearica is more extensive than in Grus (or Aramus). In Balearica the inserting tendon bifurcates, and one portion inserts on the fascia of M. adductor mandibulae medius, while the other turns anteriorly and inserts on the mandible. Grus resembles Aramus in having an undivided inserting tendon and in having the insertion independent and entirely on the mandible. Both cranes differ from Aramus in not having the inserting tendon penetrate the medial part of M. adductor mandibulae medius.

In the Rallidae the origin from the temporal fossa is lacking (present in Aramus), and the orbital origin is larger than in Aramus, occupying about half the posterior wall. The two rallids differ from Aramus in having the inserting tendon bifurcated, unossified, and not penetrating M. adductor mandibulae medius.

Summary. The Rallidae are distinct from the other two families in having the origin arising almost entirely from the orbit and in lacking the portion from the temporal fossa, which is a large portion of the origin in the limpkin and is

the main origin in the cranes. Bifurcation in the inserting tendon has perhaps arisen independently in _Balearica_ and the rails, since no such division occurs in _Aramus_ or _Grus_.

17. _M._ _pseudotemporalis_ _bulbi_

Small, strap-like muscle of soft texture and brownish coloration. Located in anteroventral region of temporal fossa and posterolateral region of orbit. Attaches to cranium, to muscle on posterior wall of orbit, and to connective tissue associated with lacrimal gland.

Ventral end deep to portions of _M._ _adductor_ _mandibulae_ _externus_ _superficialis_, _M._ _adductor_ _mandibulae_ _externus_ _medialis_, and lateral part of _M._ _adductor_ _mandibulae_ _medius_. Middle of belly superficial to middle of lateral face of _M._ _pseudotemporalis_.

Origin. Arises fleshily from narrow, small area of cranium ventral to foramen ovale, just medial to dorsal edge of quadrate.

Insertion. Muscle terminates, just medial to postorbital process, with fleshy attachment to posteroventral part of lacrimal gland, by attachment of connective tissue fibers onto muscle tissue superficial to anterior face of _M._ _pseudotemporalis_, and by attachment onto fascia covering posteroventral surface of eyeball.

Action. Uncertain; may pull on lacrimal gland and thereby aid in discharging its secretions.

Comparisons. In the Gruidae, the origin in _Balearica_ is from the anterior edge of the temporal fossa, and in _Grus_

it arises from an area of the temporal fossa slightly dorsal to that of *Balearica* (in *Aramus* it arises from a location just anteroventral to the temporal fossa). In *Balearica* the origin is posteroventral to the origin of *M. pseudotemporalis*, but posterior to that origin in *Grus* (and ventral to it in *Aramus*).

In the Rallidae this muscle is essentially the same as in *Aramus*.

Summary. There is only a slight difference between the two cranes in the location of the origin of this muscle, and both are slightly different from *Aramus*. Otherwise the muscle in the cranes is quite like that of *Aramus*, and in the rallids the whole muscle is essentially the same as in the limpkin.

18. *M. pterygoideus ventralis*

Large jaw muscle forming an elongate triangle with larger end posterior; divided except at insertion into superficial and deep layers. Muscle covers all except dorsal surface of posterior end of mandible and extends dorsad to occupy region dorsal to buccal cavity. Attaches to mandible, to pterygoid, and to palatine.

The variability in the pterygoid muscles in closely related species was shown by Lakjer (1926) and is corroborated in this study. Fisher and Goodman (1955) state that all parts of their *M. pterygoideus ventralis* and *M. pterygoideus dorsalis* may arise embryologically from a single muscle mass, and some workers have synonymized all parts as components of

one muscle (Edgeworth, 1935, _M_. _adductor_ _mandibulae_ _internus_; Gadow, 1893, _Mm_. _pterygoidei_). From the similar orientation of the bundles in _Grus_ (Fisher and Goodman, 1955, fig. 7) it seems more reasonable to include the lateral part of _M_. _pterygoideus_ _dorsalis_ with _M_. _pterygoideus_ _ventralis_, and that part is in fact fused with the adjacent part of _M_. _pterygoideus_ _ventralis_ in all the genera dissected in this study.

The classification of Fisher and Goodman is retained here, for convenience, in spite of its artificial nature. However, the terminology of the attachments is reversed, since the pterygoids and palatines are more effectively moved by contraction of these muscles than is the mandible.

Posterior end on both lateral and medial sides of mandible lies deep to muscle sheet composed of _M_. _stylohyoideus_ and _M_. _constrictor_ _colli_, and portion along medial edge of mandible deep to _M_. _geniohyoideus_. Posterior end contacts edge of insertion of _M_. _depressor_ _mandibulae_, and portion on lateral side of mandible contacts posteroventral edge of insertion of lateral part of _M_. _adductor_ _mandibulae_ _medius_. Side of deep layer apparently fused to entire length of lateral part of _M_. _pterygoideus_ _dorsalis_. Superficial to insertion of medial part of _M_. _adductor_ _mandibulae_ _medius_ on medial side of mandible. Deep layer superficial to medial part of _M_. _pterygoideus_ _dorsalis_ and to _M_. _protractor_ _pterygoideus_. Superficial layer superficial to all of deep layer except a portion of lateral edge on ventral side.

Origin. Superficial layer arises partly fleshily and partly by flattened, ossified tendon, from posteroventral

corner of lateral face of mandible. Additional fleshy and tendinous origins arise from lateral, ventral, and medial edges of posterior face of mandible. Portion of origin on medial side of mandible common to both superficial and deep layers. This origin is mostly fleshy but includes several ossified tendons attaching to dorsomedial tip of internal articular process.

Insertion. Superficial layer inserts fleshily on entire ventrolateral trough of palatine, tendinously on ventral and posterior edges of ventrolateral wing of palatine, and fleshily on ventral surface of medial end of pterygoid. Deep layer inserts fleshily on dorsolateral surface and tendinously on dorsomedial edge of palatine.

Action. Retracts palatine and pterygoid and depresses upper jaw.

Comparisons. In the Gruidae the deep layer in Balearica (and Aramus) is simple, but in Grus it is further divided into distinct lateral and medial parts. The superficial layer in Grus is uniquely specialized in having a strong, silvery aponeurosis over its insertion. In both cranes the superficial layer is superficial to all of the deep layer (to all but the lateral edge of the deep layer in Aramus). In Balearica (and Aramus) the lateral surface of the deep layer is completely fused to M. pterygoideus dorsalis but is entirely separate in Grus. In Balearica (and Aramus) most of the portion on the lateral surface of the mandible is covered by M. stylohyoideus and M. constrictor colli, but very little

of this portion is covered by _M. stylohyoideus_ and none by _M. constrictor colli_ in _Grus_. In _Balearica_ the superficial and deep layers are fused at the origins and along their lateral edges (in _Aramus_ the two layers are fused only at their origins), but in _Grus_ the two layers originate separately. _Balearica_ (and _Aramus_) have a single insertion of the superficial layer, but there are two separate insertions in _Grus_. _Balearica_, and apparently _Grus_, differ from _Aramus_ in lacking ossified tendons in the origin.

In the Rallidae, the muscle in _Rallus_ (and _Aramus_) is composed of a superficial layer and a single deep layer, but in _Fulica_ the portion corresponding to the lateral part of the deep layer of _Grus_ is distinct, and the bundles corresponding to the medial part of the deep layer are fused into one muscle with the superficial layer.

In _Fulica_ alone some of the muscle is deep to the anterior, free portion of _M. geniohyoideus_, as a result of greater thickness and more posterior attachment of that muscle.

Summary. For the details discussed above, _Balearica_ and _Grus_ show little agreement, but _Aramus_ and _Balearica_ are quite similar. The division in the deep layer in _Grus_ represents the most striking specialization, and a somewhat similar specialization is present in _Fulica_. The muscle in _Rallus_ is quite like that of _Aramus_ and differs from that of _Fulica_ mainly in the connections of the various portions.

19. *M. pterygoideus dorsalis*

Medium-sized and flattened muscle, oblanceolate in lateral view; partially divided into dorsal and ventral divisions. Located just anteromedial to angle of jaw. Attaches to mandible, to pterygoid, and to palatine.

Lies deep to *M. pterygoideus ventralis*. Adjoins posterior edge of insertion of medial part of *M. adductor mandibulae medius* and posterior edge contacts *M. protractor pterygoideus*.

Origin. Arises fleshily from wide area of medial and dorsomedial part of mandible, between posterior edge of insertion of *M. adductor mandibulae medius* and posterior edge of mandible. Dorsomedial portion of origin occupied by partially distinct dorsal section.

Insertion. Inserts tendinously and fleshily on all but posterior surface of pterygoid. Partially separated dorsal division inserts on posterior end of palatine, just anterior to previous attachment.

Action. Depresses upper jaw by retracting palatine and pterygoid.

Comparisons. In the Gruidae, the muscle in *Balearica* (and *Aramus*) is simple, but in *Grus* it is comprised of distinct lateral and medial parts. The representative of the lateral part in *Balearica* (and *Aramus*) is apparently completely fused into the lateral edge of the deep layer of *M. pterygoideus ventralis*, and the medial part represents the sole remnant of the muscle in this crane. In *Balearica* (and *Aramus*) the muscle is partially divided into dorsal and

ventral sections, but no division occurs in the corresponding part in _Grus_. In _Balearica_ (and _Aramus_) the origin extends from the medial onto the dorsomedial portion of the mandible, but the corresponding part in _Grus_ arises only from the medial side. In _Balearica_ (and _Aramus_), but not in _Grus_, a portion of the insertion is on the dorsal side of the pterygoid.

In the Rallidae the muscle differs from that of _Aramus_ in having no evidence of the partial separation of the muscle into dorsal and ventral sections and no attachment to the palatine. In _Rallus_ (and _Aramus_) the origin does not overlap the deep part of _M. adductor mandibulae medius_, but in _Fulica_ the origin is wider and overlaps the posterior edge of the deep part of that muscle.

Summary. _Grus_ seems specialized since the points by which it differs from _Balearica_ are strikingly alike in _Aramus_ and _Balearica_, and even like those in the two rallids. _Grus_ alone has a separate lateral part, and the partial division of the muscle in _Aramus_ and _Balearica_ is not found in the corresponding, medial part in _Grus_. In _Aramus_ and _Rallus_ the muscle is nearly identical, and differs only slightly in _Fulica_.

20. _M. protractor pterygoideus_

Small muscle composed of sheet-like ventral part and somewhat thicker dorsal part. Ventral part located posterior to pterygoid; dorsal part located just posterodorsal to pterygoid and posteroventral to orbital process of quadrate. Attaches to basitemporal plate, to ventrolateral region of orbit, and to pterygoid.

Anterior extent of ventral part in contact with _M._ _pterygoideus_ _dorsalis_ and partly deep to posterior edge of _M._ _pterygoideus_ _ventralis_. Dorsal part ventral to _M._ _protractor_ _quadratus_.

Origin. Ventral part arises fleshily from anterolateral area of basitemporal plate, adjacent to anterior edge of insertion of medial part of _M._ _rectus_ _capitis_ _ventralis_. Dorsal part originates from lateral depression in basisphenoid and from adjacent ventromedial area of orbit just anteromedial to origin of _M._ _protractor_ _quadratus_.

Insertion. Ventral sheet inserts fleshily along medial edge of entire length of pterygoid bone. Dorsal sheet has mostly fleshy insertion on posterodorsal side of posterior end of pterygoid bone.

Action. Raises maxilla by pulling pterygoid forward.

Comparisons. In the Gruidae the muscle is composed of only one part (definite dorsal and ventral parts in _Aramus_), and the insertion is on the anterior third of the pterygoid (on the full length of the pterygoid in _Aramus_).

In the Rallidae (as in _Aramus_) the muscle is in two distinct parts, and the ventral sheet inserts on the full length of the pterygoid. In _Rallus_ the dorsal part is enclosed by fleshy fibers of _M._ _protractor_ _quadratus_, but the same part is ventral to that muscle in _Fulica_ (and _Aramus_). In _Rallus_ the dorsal part is wide at its origin and inserts by a slender but strong tendon. In _Fulica_ (and _Aramus_) the origin of this part is narrower, and the insertion is fleshy and wider.

<u>Summary</u>. The cranes are distinct from the limpkin and the rails in having the muscle undivided, with a more restricted insertion. <u>Rallus</u> appears specialized in having the dorsal part enclosed, with a wide origin and a narrow and tendinous insertion. In <u>Aramus</u> and <u>Fulica</u> the enclosure of the dorsal part is lacking, the origin is narrower, and the insertion is wider and fleshy.

The stronger insertion in <u>Rallus</u> may be associated with feeding habits, such as gaping under pressure when the bill is probed into mud, but a corresponding enlargement of <u>M. depressor mandibulae</u>, as occurs in some passerines with strong gaping adaptations (Beecher, 1951a), is lacking.

21. <u>M. protractor quadratus</u>

Small, thick muscle composed of very short fibers. Located in small space between cranium and orbital process of quadrate. Attaches to cranium and to quadrate.

Deep to belly of <u>M. pseudotemporalis</u>. Dorsal to lateral portion of dorsal part of <u>M. protractor pterygoideus</u>, and posterior to medial portion of same muscle.

<u>Origin</u>. Arises fleshily from area of cranium immediately medial to orbital process of quadrate. Origin includes small section of posteroventral region of orbit. Medial extend of origin posterior to, and in contact with, medial extend of origin of dorsal part of <u>M. protractor pterygoideus</u>.

<u>Insertion</u>. Has fleshy insertion on entire medial surface of orbital process of quadrate.

Action. Raises maxilla by rotating lower end of quadrate forward.

Comparisons. In the Gruidae the origin in *Balearica* (and *Aramus*) is larger and more ventrally located than in *Grus*. The insertion in *Balearica* (and *Aramus*) is on all of the medial surface of the orbital process of the quadrate, but on only the posterior edge of the medial surface of that process in *Grus*.

In the Rallidae the muscle in *Rallus* encloses the dorsal part of *M. protractor pterygoideus* but is located entirely dorsal to that muscle in *Fulica* (and *Aramus*).

Summary. The differences in the muscle in the two cranes are very slight, but a closer resemblance between *Aramus* and *Balearica* is apparent, in spite of the small differences involved. *Rallus* appears more specialized in having the muscle located farther ventrally than in *Fulica* or *Aramus*, as a result of which is partially encloses another protractor muscle.

This may also be associated with gaping adaptations, since the muscle aids in opening the mouth by raising the maxilla.

Muscles of the Hyoid

22. *M. constrictor colli*

Thin, partly double, dermo-osseous sheet with orientation of bundles anteromedial at anterior end, changing to posteromedial and then to transverse along neck. Posterior

bundles loosely connected and gradually fade out posteriorly. Extends from anterior end of basihyal bone posteriad across throat, and lines skin of entire neck, nearly to posterior end. Attaches to mandible, to connective tissue in mid-line, to M. stylohyoideus, to M. dermo-temporalis, and to skin.

This muscle may include the posterior sheet of M. mylohyoideus (also called M. serpio-hyoideus), which Fisher and Goodman (1955) stated could not be found in Grus americana.

Fused to other member of pair by connective tissue in mid-line. Extreme anterior end deep to M. intermandibularis. Superficial on mandible to M. pterygoideus ventralis and to hyoid and tracheal muscles in region of throat. Superficial to posterior edge of M. dermo-temporalis and to M. tracheohyoideus through most of length of neck.

Origin. Arises by two sheets that join at posteroventral corner of mandible. One sheet attaches to superficial and one to deep side of posterior edge of mandible. Deep sheet arises in common with M. stylohyoideus, in contact with insertion of M. depressor mandibulae. Both sheets superficial to origin of M. pterygoideus ventralis.

Insertion. In region of throat inserts on connective tissue in mid-line and loosely onto skin. Posterior to mandible transverse bundles insert only on skin.

Action. Constricts and raises musculature of throat and hyoid apparatus, and constricts skin on ventral side of neck.

Comparisons. In the Gruidae the sheet is thinner than in Aramus. In Balearica it has fewer contractile components

than in *Aramus*, and in *Grus* it has even fewer muscular fibers. In *Balearica* the muscle arises by a deep fascial sheet and a superficial muscular sheet, but in *Grus* only one sheet is present (*Aramus* has two sheets, both muscular). In the cranes only the superficial sheet contributes to the origin of *M. stylohyoideus* (in *Aramus* both sheets contribute equally to that origin). In both cranes the muscle lies between the posterior end of the basihyal bone and the seventh cervical (in *Aramus* it extends from the anterior end of the basihyal nearly to the posterior end of the neck). In *Balearica* (and *Aramus*) the muscle gradually fades into the skin posteriorly, but in *Grus* it ends more abruptly on tracheal fascia and cervical muscles.

In the Rallidae the contractile content of the muscle is equal to that of *Aramus*, and in *Fulica* the thickness is even greater. The division into two sheets is similar in both rallids, but the inner one is weaker in *Rallus*. In *Rallus* only the deep sheet, and in *Fulica* only the superficial sheet, contributes to the origin of *M. stylohyoideus*. In both rallids the bundles just posterior to the jaw pass further dorsad than in *Aramus* and even reach the mid-dorsal line in the region of the frontal bones. In the two rails the anterior end of the muscle is located more posteriorly than in *Aramus*, lying about 5 mm posterior to the posterior end of the basihyal bone. In both rallids the muscle ends on the skin of the neck, but in *Rallus* it extends about half the length of the neck, and in *Fulica* it extends the full length.

Summary. This constrictor sheet is well developed in Aramus and Rallus and is highly developed in Fulica. It is reduced in the cranes, especially in Grus. The deep sheet of the origin is better developed in Aramus than in the rallids and entirely lacks contractile fibers in the gruids. In the limpkin the anterior end of the muscle is anterior to the position in the cranes and considerably anterior to that in the two rallids. In the cranes the muscle sheet barely extends onto the neck, but covers at least half the neck in the other three genera. This constrictor sheet appears to have been variously modified in the species studied, but in extent and development the muscle in Aramus finds somewhat better agreement in the rallids than in the gruids.

23. M. intermandibularis

Thin muscle sheet with bundles oriented essentially transversely and gradually becoming indistinct at anterior end. Located between rami of mandible. Attaches to mandible, to connective tissue in mid-line, and loosely to skin.

Fused to other member of pair by connective tissue in mid-line. Posterolateral edge deep to anterior end of M. geniohyoideus. Superficial to M. genioglossus, and posterior end superficial to anterior ends of M. constrictor colli and M. stylohyoideus.

Origin. Takes fleshy origin from dorsomedial edge of mandible on line extending from gonys to about level of middle of basihyal bone.

Insertion. Inserts in mid-line on same connective tissue to which M. constrictor colli attaches, on line extending posteriad from gonys to point 10 mm beyond posterior end of basihyal bone.

Action. Raises anterior hyoid musculature and floor of mouth.

Comparisons. In the Gruidae the muscle is quite reduced, being composed of a very thin contractile sheet in Balearica and having only a few muscular fibers in Grus (in Aramus the entire sheet is muscular and thicker). In Balearica contractile fibers are indistinct in the anterior half of the bill and in Grus are not present at all except at the posterior end of the sheet. In Balearica the posterior end of the origin is slightly anterior to that of Aramus, but the posterior end of the insertion is considerably posterior to that point in Aramus, being about even with the posterior end of the basihyal bone.

In the Rallidae the thickness and contractile nature of the muscle agrees with that of Aramus, but the muscle is thicker in Fulica. In both rallids the muscle sheet becomes thinner, with its anterior regions more closely attached to the skin than in Aramus. In both rallids the posterior ends of the origin and the insertion are located slightly posterior to the corresponding locations in Aramus.

Summary. This muscle is quite reduced in the gruids, especially so in Grus. It is well developed in Aramus and the rallids, especially in Fulica. The position of the posterior edge of the muscle in Aramus is intermediate between

that of the cranes and that of the rails. In _Aramus_ and the gruids the anterior end of the sheet is more closely attached to skin than in the rallids. The differential development of this muscle in the three families is parallel to that of _M. constrictor colli_, and as is found in the latter muscle, _Aramus_ agrees better with the rallids than with the gruids.

24. _M. geniohyoideus_

Very elongate, thin band of muscle. Located mainly beneath floor of mouth along medial side of mandible, but extends posteriad around posteroventral corner of mandible to lie along posterolateral edge of cranium. Attaches to mandible, to floor of mouth, and to thyrohyals.

Middle of belly deep to _M. constrictor colli_, and posterodorsal tip deep to _M. dermo-temporalis_. Anterior half superficial to lateral edge of _M. intermandibularis_, and middle of belly superficial to ventral side of _M. pterygoideus ventralis_. Posterior portion superficial to portion of _M. ceratoglossus_, and posterodorsal portion passes over _M. rectus capitis ventralis_ and _M. rectus capitis lateralis_.

Origin. Arises fleshily from elongate area along dorsomedial side of ramus of mandible. Extends from level of posterior end of mandibular foramen to about level of anterior half of nostril, lying just ventral to origin of _M. intermandibularis_. Posterior end of attachment lies between _M. pterygoideus ventralis_ and mandible.

Insertion. Posterior end passes onto greater cornu of hyoid, partially encloses ceratohyal, attaches loosely to

posterior end of that bone and to anterior end of epihyal, and finally inserts fleshily onto entire surface of posterior end of epihyal and its cartilaginous extension.

According to Fisher and Goodman (1955) the mandibular attachment is the insertion, and the thyrohyal attachment is the origin. Since the latter attachment is the more movable, it is considered here as the insertion and the mandibular attachment as the origin.

Action. Protracts tongue by pulling hyoid apparatus forward.

Comparisons. In the Gruidae, *Balearica* is unique in having an additional small lateral slip that arises from the lateral face of the mandible. The gruids differ from *Aramus* in having the muscle connect to *M. dermoglossus*, but this union is inconstant in *Grus*. In *Balearica* the origin of the main slip is long and extends slightly farther anteriorly than in *Aramus*, but in *Grus* this attachment (called insertion by Fisher and Goodman, 1955) is much shorter. In *Balearica* (and *Aramus*) the posterior end encloses the ceratohyal but attaches only loosely to the posterior end. In *Grus* this attachment is more extensive, as is the epihyal attachment (called origin by Fisher and Goodman, 1955). The small lateral slip, present only in *Balearica*, fuses with the main slip at the side of the distal end of the insertion. The individual variation mentioned for this muscle in *Grus* is not found in *Aramus*.

In the Rallidae a small lateral slip is found in *Rallus* but not in *Fulica*. Both rallids agree with *Aramus* in lacking

connection of the muscle to *M. dermoglossus*. The combined origin of the two slips, from the lateral face of the mandible, is short and deep in *Rallus* and corresponds to the origin of the single slip in *Fulica* (in *Aramus* a single origin is also present, but it is very much longer and shallower and comes from the medial side of the mandible). In both rallids the enclosure of the ceratohyal and the insertion on the epihyal are both similar to conditions in *Aramus*. The small slip in *Rallus* fuses with the posterior end of the insertion of the main slip.

Summary. This muscle agrees in the cranes and the limpkin in having a rather long, shallow origin, whereas in the rallids the origin is very short but deep. It seems that the more anterior extension would allow greater protraction of the tongue in the cranes and the limpkin. The division into two slips seems to have arisen independently, but strikingly similarly, in *Balearica* and *Rallus*. The small lateral slip could act to pull the distal end of the cornu laterad and perhaps to brace the protracted tongue.

25. *M. stylohyoideus*

Very long, narrow group of bundles arising as anterodorsal edge of sheet of *M. constrictor colli*. Located in ventrolateral region of throat. Attaches to mandible, to *M. constrictor colli*, and to entoglossum.

Anterior end deep to *M. constrictor colli*, *M. intermandibularis* and *M. genioglossus*. Posterior end fused with both sheets of *M. constrictor colli*, and anterior half lies

alongside *M. ceratoglossus lateralis*. Posterior end superficial to posterior end of *M. ceratoglossus inferior* and to *M. pterygoideus ventralis*. Middle of belly passes over *M. geniohyoideus*.

Origin. Arises as part of both sheets of *M. constrictor colli*, from dorsomedial and dorsolateral corners of posterior edge of mandible.

Insertion. Separates from *M. constrictor colli* as it passes under ventral edge of mandible and follows side of *M. ceratoglossus lateralis* to insert fleshily on tendon of that muscle and on posterolateral corner of entoglossum.

Action. One muscle turns tongue laterad, but both together retract tongue and perhaps raise it.

Comparisons. In the Gruidae the muscle in *Balearica* is much thinner and flatter than in *Grus* (or *Aramus*). In *Balearica* the origin merges imperceptibly with *M. constrictor colli*, but in *Grus* (and *Aramus*) it appears as separate muscle. In both cranes the muscle agrees with that of *Aramus* in arising partly from the mandible, but differs in having no origin from the medial side. *Grus* is unique in having a portion arise from the opisthotic process. In *Balearica* a part of the insertion (and all of the insertion in *Aramus*) is on the posterolateral corner of the entoglossum, but the remainder of the insertion in *Balearica* is on the dorsolateral portion of the anterior end of the basihyal. In *Grus* the insertion is on the most anterolateral surface of the ceratohyal, at the articulation between that bone and the

basihyal. The more posterior location of the insertion in Grus would result in less effective movement of the tongue, so that the main function in this genus is apparently retraction of the hyoid apparatus.

In the Rallidae the muscle in Rallus is small and bandlike as in Aramus, but in Fulica it is very thick and somewhat rectangular in cross section. In Rallus (and Aramus) the muscle originates partly from both sheets of M. constrictor colli, but no connection with that muscle is present in Fulica, in which the origin is entirely from the side of the posterior end of the mandible. In Rallus the anterior end of the muscle is variable but usually divides into two portions, one inserting on the anteromedial extent of the ceratohyal and the other usually inserting on the dorsal side of the posterior portion of the basihyal bone, although this anterior insertion is sometimes on the ceratohyal, just anterior to the previous one. In Fulica the bundles of the anterior end of the ceratohyal and the posterior end and lateral side of the basihyal (in Aramus it inserts on the entoglossum). In both rallids the action is probably retraction of the whole hyoid, rather than direct movement of the tongue as in Aramus. The larger muscle in Fulica indicates a stronger action.

Summary. This muscle is variable and apparently quite subject to specialization among the genera studied. The shape and size of the belly are nearly uniform in the genera other than Fulica, in which the muscle is considerably larger.

The origin is from both lateral and medial faces of the mandible in the limpkin and in _Rallus_, but arises only from the side in _Fulica_ and the gruids. The variable insertion is similarly located in _Aramus_ and _Balearica_, but it is much farther posterior in _Grus_ and the rallids. In view of the more anterior insertion, it seems that the main function in _Aramus_ and _Balearica_ is to move the tongue laterad and raise it, but in _Grus_ and the rallids it must retract the hyoid apparatus.

26. _M. genioglossus_

This muscle sheet is not present in _Aramus_, and no contractile fibers are found in the membranous floor of the mouth. _M. intermandibularis_, largely absent or reduced to fascia in _Grus_, is well developed in _Aramus_ and lies just superficial to the presumed location of _M. genioglossus_. The former sheet has an origin similar to that described for the latter muscle, but its insertion is not on the floor of the mouth or the entoglossum, and therefore it is an entirely different muscle, even though it probably has a somewhat similar function.

Comparisons. In the Gruidae, the muscle is absent in _Balearica_ but present in _Grus_. In _Grus_ the muscle is a thick, widely triangular sheet, the lateral edge of which lies between _M. geniohyoideus_ and the floor of the mouth. It arises from a small area on the inner side of the mandible, dorsal to the insertion of _M. geniohyoideus_, and flares widely to insert on the floor of the mouth and on the posterior half

of the entoglossum. The anterior ends of the corresponding right and left muscles meet in the mid-line of the entoglossum. The apparent function of the two muscles is to raise the tongue and floor of the mouth, although one muscle alone could turn the tongue laterad.

The absence of the muscle in _Balearica_, compared to the presence in _Grus_, may be correlated with the more anterior insertion of _M_. _stylohyoideus_, for lateral movement of the tongue, in _Balearica_ (and _Aramus_). In _Grus_ that insertion is considerably posterior to the tongue, but a similar function is apparently served in that crane by _M_. _genioglossus_.

In the Rallidae the muscle is absent in _Rallus_ but well developed in _Fulica_. In _Fulica_ the origin extends along all but the anterior end of the dorsomedial edge of the mandibular ramus, just dorsal to the origin of _M_. _intermandibularis_. The insertion is on the floor of the mouth and the base of the entoglossum.

Summary. The muscle is absent in _Aramus_, _Balearica_, and _Rallus_ but is well developed in _Grus_ and even more so in _Fulica_. Its absence in _Aramus_ and _Balearica_ may be functionally correlated with an insertion of _M_. _stylohyoideus_ much farther anterior than in _Grus_. This correlation is not apparent in the two rallids, even though the insertion of _M_. _stylohyoideus_ is usually anterior to that of _Grus_. This muscle is apparently modified in association with specialized feeding habits. The well-developed condition, at least in _Fulica_, is probably associated with pressing the tongue

against the papillae in the roof of the mouth in order to grasp vegetation.

27. _M. dermoglossus_

This muscle is absent in _Aramus_.

Comparisons. In the Gruidae the muscle is present. In _Balearica_ and _Grus_ it is a short, thin sheet arising from the basihyal bone. In _Balearica_ the origin is from the lateral face of the middle of the bone but from the dorsolateral corner of the anterior end in _Grus_. The insertion in both cranes is on the wall of the pharynx, but in _Balearica_ it also merges with _M. constrictor colli_ and is joined by the small sheet of the posterior part of _M. ceratoglossus inferior_, arising from the middle of the ceratohyal. Contraction of the muscle would draw the lateral pharyngeal walls forward, perhaps during swallowing.

According to Fisher and Goodman the muscle arises from the pharynx and inserts on the basihyal. Since the pharyngeal attachment is the more movable, the origin and insertion should be reversed, as they are described above.

In the Rallidae the muscle is absent.

Summary. The muscle is present in Gruidae, but in _Aramus_ and Rallidae it is absent.

28a. _M. ceratoglossus lateralis_

Very elongate and somewhat rounded. Located on lateral and dorsal aspects of hyoid apparatus, from middle of cornu to base of entoglossum. Attaches to ceratohyal, loosely to

basihyal, to _M. stylohyoideus_, to _M. hypoglossus rectus_, and to entoglossum.

Posterior tip deep to posterior end of _M. ceratoglossus inferior_ and also to part of _M. geniohyoideus_. Most of muscle lies deep to sheets of _M. constrictor colli_ and _M. intermandibularis_. Courses alongside _M. hypoglossus obliquus_ and _M. hypoglossus rectus_. Lies medial to insertion of _M. stylohyoideus_. Located superficial to combined bellies of _M. thyroglossus_ and _M. thyrohyoideus_.

Origin. Arises fleshily from dorsal and lateral surfaces of anterior two-thirds of ceratohyal, and attaches loosely to side of basihyal.

Insertion. Alongside _M. hypoglossus obliquus_ belly narrows into small tendon that continues anteriad to receive portion of insertion of _M. stylohyoideus_, to attach to side of _M. hypoglossus rectus_, and finally to merge with posterolateral region of entoglossum.

Action. One muscle bends tongue ventrolaterad, and both together pull tongue downward.

Comparisons. In the Gruidae the muscle is superficial to the posterior end of the posterior part of _M. ceratoglossus inferior_, instead of deep to it as in _Aramus_. In _Balearica_ (and _Aramus_) the muscle arises from the dorsal and lateral surfaces of the ceratohyal, but in _Grus_ it arises from the ventrolateral and dorsolateral surfaces. In both cranes (and _Aramus_) the origin is from the anterior two-thirds of the ceratohyal. The points of insertion in both gruids agree

with those of _Aramus_, but in _Balearica_ (and _Aramus_) attachment is by a tendon, and in _Grus_ the muscle is fleshy throughout.

In the Rallidae the origin is from all but the ventral surface of the full length of the ceratohyal bone (in _Aramus_ it arises from the dorsal and lateral surfaces of the anterior two-thirds). In both rallids the small tendon begins at about the middle of the belly and lies superficially on the belly (in _Aramus_ the tendon arises much farther forward, at the anterior end of the belly). The insertion in both rallids is essentially the same as in _Aramus_. In _Fulica_ (and _Aramus_) the inserting tendon receives part of the insertion of _M. stylohyoideus_, but no such connection exists in _Rallus_.

Summary. _Aramus_ differs from the rallids but resembles the gruids in having a smaller area of origin and a shorter tendon of insertion. However, _Grus_ is unique among the genera examined in having the insertion entirely fleshy.

28b. _M. ceratoglossus inferior_

Rather short band of muscle. Lies against ventral side of hyoid musculature between posterior ends of mandibular rami. Attaches to ceratohyal and to connective tissue in mid-line.

The single slip in _Aramus_ corresponds to the posterior part in _Grus_, but the lateral and medial parts found in that crane are lacking in the limpkin.

Muscle lies entirely deep to _M. constrictor colli_, and posterior end also deep to _M. geniohyoideus_. Lies

superficial to *M. ceratoglossus lateralis* on ceratohyal, and belly lies superficial to *M. thyroglossus* and *M. thyrohyoideus*.

Origin. Arises fleshily from ventral surface of ceratohyal, beneath *M. geniohyoideus*, from line of origin about as long as width of muscle.

Insertion. Inserts in ventral mid-line, deep to area of overlap of, and on connective tissue that forms insertion of, *M. constrictor colli* and *M. intermandibularis*.

Action. May act to raise or protract hyoid apparatus, or both.

Comparisons. In the Gruidae, *Balearica* agrees with *Aramus* in having the muscle represented by only the posterior part, which is a band-like sheet. In *Grus* the muscle includes lateral and medial parts, and the posterior part is more elongate and rounded. In *Grus* both the lateral and medial parts arise from the anterior end of the ceratohyal, and the lateral part inserts on *M. hypoglossus rectus* and on the ventrolateral corner of the entoglossum, while the medial part inserts on the middle of the basihyal. In *Balearica* the sole (posterior) part arises from the entire surface of the posterior one-third of the ceratohyal (in *Aramus* it arises from a line about the width of the muscle), but in *Grus* the corresponding origin is apparently much smaller. The insertion of the posterior part in *Balearica* (and *Aramus*) is on connective tissue in the ventral mid-line, but in *Grus* it is on fascia over the junction of the basihyal and urohyal.

In the Rallidae the muscle is somewhat thicker in _Fulica_ than in _Rallus_ (or _Aramus_). Points of attachment agree in the rails and the limpkin.

Summary. The muscle differs only in thickness and extent of origin in the genera other than _Grus_, but in that crane it includes two additional parts. The one part common to all genera inserts in _Grus_ in an entirely different location from that of _Balearica_ and the non-gruids. In _Aramus_, _Balearica_, and the two rallids the muscle apparently functions in raising the hyoid apparatus and perhaps in protracting it, but in _Grus_ the only apparent function is to adduct the cornua of the hyoid.

29. _M_. _hypoglossus_ _rectus_

Small, triangular muscle with attenuate anterior end. Closely fused with opposite member in mid-line, and two muscles have common tendon anteriorly. Occupies ventral face of posterior end of entoglossum and median strip along ventral surface of tongue. Attaches to entoglossum and to _M_. _ceratoglossus_ _lateralis_.

Right and left muscles loosely connected across midline. Completely deep to _M_. _intermandibularis_. Posterior end adjacent to insertions of _M_. _stylohyoideus_ and _M_. _ceratoglossus_ _lateralis_.

Origin. Arises fleshily from veneral face of posterior end of entoglossum, and to lesser extent, from inserting tendon of _M_. _ceratoglossus_ _lateralis_.

Insertion. Right and left muscles have common insertion, by narrow and strap-like tendon that extends along ventral mid-line of tongue and attaches onto ventral side of anterior portion of entoglossum.

Action. Causes tongue to curve downward.

Comparisons. In the Gruidae the muscle has fewer fleshy fibers and more extensive tendons that in _Aramus_. In _Balearica_ (and _Aramus_) the main origin comes from the entoglossum, with a lesser origin from _M_. _ceratoglossus_ _lateralis_, but in _Grus_ it arises mainly from the lateral part of _M_. _ceratoglossus_ _inferior_, which is lacking in _Balearica_ (and _Aramus_). In _Grus_ the inserting tendon connects to _M_. _genioglossus_, which is also absent in _Balearica_ (and _Aramus_). The length of the inserting tendon varies with the length of the tongue in the two cranes and the limpkin.

In the Rallidae the muscle differs from that of _Aramus_ in being slightly longer and narrower, with closer connection to the inserting tendon of _M_. _ceratoglossus_ _lateralis_. The actual size of the belly is similar in both rallids in spite of differences in the length of the tongue, but the tendon is longer in _Rallus_. In _Fulica_ only, the paired bellies do not contact across the mid-line.

Summary. The pattern of the muscle is rather constant in all genera studied, even though the length and shape of the tongue vary considerably. Differences in the length of the tongue are reflected in differences in the length of the tendon of insertion. In _Grus_ the muscle connects to two muscles not present in the other genera.

30. *M*. *hypoglossus* *obliquus*

Small, triangular muscle with lateral and ventral faces at right angles to each other. Located on lateral and ventral faces of anterior end of basihyal. Attaches to basihyal and to entoglossum.

Right and left muscles loosely fused across mid-line. Entirely deep to *M*. *intermandibularis*. Lies just medial to anterior portion of *M*. *ceratoglossus* *lateralis*, ventromedial to insertion of *M*. *stylohyoideus*, and just posterior to *M*. *ceratoglossus* *inferior*.

Origin. Arises fleshily from lateral and medial faces of anterior half of basihyal.

Insertion. Attaches fleshily to ventral and lateral edges of posterior end of entoglossum, adjacent to posterior edges origin of *M*. *hypoglossus* *rectus*.

Action. One muscle pulls tongue ventrolaterad, but both muscles together depress distal portions of tongue.

Comparisons. In the Gruidae the muscle in *Balearica* is thinner than in *Grus* (or *Aramus*), but it lies along the full length of the ventral side of the basihyal instead of only the anterior two-thirds as in *Grus* (or the anterior half as in *Aramus*). In *Grus* the muscle is deep to the anterior tendon of the lateral part of *M*. *ceratoglossus* *inferior* and *M*. *genioglossus*, and lies medial and superficial to the medial part of *M*. *ceratoglossus* *inferior*; none of these muscles are present in *Balearica* (or *Aramus*). The origin is more extensive in *Balearica* than in *Grus* (or *Aramus*). *Grus* is unique

in having some tendinous components to the origin. In _Balearica_ (and _Aramus_) the insertion is on the ventral and lateral edges of the posterior end of the entoglossum, but in _Grus_ the insertion is narrower, on only the ventrolateral corner of the entoglossum. In _Balearica_ only, the insertion is partly on the medial side of the inserting tendon of _M. ceratoglossus lateralis_.

In the Rallidae the muscle is larger in _Rallus_ than in _Fulica_ (or _Aramus_), but the shortened basihyal in the coot makes comparison difficult. In _Rallus_ the muscle occupies the full length of the basihyal, but in _Fulica_ it does not cover the posterior end (in _Aramus_ it covers only the anterior end). The rallids differ from _Aramus_ in having the muscle attach to the medial side of the inserting tendon of _M. ceratoglossus lateralis_; this attachment is stronger in _Fulica_.

Summary. The size and attachments of the muscle are varied among the genera studied, and there seems to be no good correlation with the length of the tongue. The muscle is longest in _Balearica_ and _Rallus_, but the tongue is short in the former and long in the latter. The muscle is shortest in _Aramus_, which has the longest tongue, and _Fulica_, which has a short tongue. However, the two genera with the shortest tongues, _Balearica_ and _Fulica_, both have close connection of the muscle to the tendon of _M. ceratoglossus lateralis_ alongside it. Such connection is very weak or lacking in the other three genera, all of which have long tongues. This

muscle is certainly more subject to specialization than is M. hypoglossus rectus.

31. M. thyroglossus
32. M. thyrohyoideus

Long and somewhat rounded, composed of two inseparable muscles, lateral M. thyrohyoideus and medial M. thyroglossus. Very narrow, entirely separate accessory slip of former muscle lies lateral to main belly. Located in ventral region of pharynx, between hyoid apparatus and larynx. Attaches to larynx, to wall of pharynx, to basihyal, to entoglossum, to urohyal, and to ceratohyal.

Muscles on each side loosely connected across mid-line. Posterior half partly deep to M. constrictor colli, M. intermandibularis, and posterior part of M. ceratoglossus inferior; anterior portion partly deep to M. ceratoglossus lateralis and M. stylohyoideus.

Origin. Main belly arises fleshily from lateral and ventral regions of anterolateral portion of cricoid cartilage, adjacent to lateral edges of M. thyroarytenoideus and M. constrictor glottidis. Small portion originates from ventrolateral wall of pharynx, posterior to attachment to cricoid, more or less continuous with portion of insertion of M. tracheohyoideus in same area. Small accessory part of M. thyrohyoideus arises separately from ventrolateral wall of pharynx.

Insertion. Belly passes dorsal to basihyal, where small fasciculi partially separate from main belly. One

fasciculus inserts on dorsolateral edge of basihyal about 2 mm anterior to posterior end of bone. Other fasciculi remain partially joined and insert fleshily on all of dorsal surface of anterior third of basihyal and on entire posteroventral edge of entoglossum. Separate accessory part of _M._ _thyrohyoideus_ inserts on junction of urohyal, basihyal, and ceratohyal.

Action. Muscles on one side reflect tongue dorsolaterad. Both sides together raise distal portions of tongue, retract hyoid apparatus, and protract larynx.

Comparisons. In the Gruidae the main origin is from the posterior edge of the cricoid cartilage (in _Aramus_ it arises from the anterolateral portion). The cranes differ from _Aramus_ in having the accessory part arise partly from the cricoid. In _Balearica_ (and _Aramus_) the muscle partially divides into fasciculi in the region dorsal to the basihyal, but it remains as a compact mass in _Grus_. In _Balearica_ (and _Aramus_) the muscle inserts on the dorsal surface of the basihyal but inserts on the lateral surface in _Grus_. In _Balearica_ (and _Aramus_), but not in _Grus_, a small fasciculus parts from the main muscle to insert on the posterior region of the basihyal. In both cranes the accessory part fuses with the main muscle instead of inserting separately as in _Aramus_.

In the Rallidae the two muscles under discussion differ from those of _Aramus_ in being separate and in lacking the accessory part, In both rallids _M._ _thyroglossus_ is wide posteriorly and narrow anteriorly, but in _Fulica_ the change from wide to narrow is more abrupt. Sometimes in _Rallus_

(and always in _Aramus_) the right and left _Mm. thyroglossi_ are loosely connected across the mid-line and lie superficial to the medial edges of _Mm. thyrohyoidei_. In _Fulica_ the two _Mm. thyroglossi_ are closely connected across the mid-line and lie superficial to all but the posterolateral portions of _Mm. thyrohoidei._ In both rallids _M. thyroglossus_ arises mainly from the posterior region of the cricoid (in _Aramus_ it arises from the anteroventral edge), and _M. thyrohyoideus_ arises from the ventrolateral region of the full length of the larynx (from the anterolateral region in _Aramus_). In both rallids _M. thyroglossus_ is short, inserting on the junction of the basihyal, ceratohyal, and urohyal bones (in _Aramus_ the main muscle is farther anterior, but the above insertion is similar to that of the accessory part of _M. thyrohoideus_). In _Rallus M. thyrohyoideus_ inserts on the dorsal face of the anterior portion of the basihyal (corresponds to the main insertion of the combined muscle in _Aramus_), but in _Fulica_ this insertion is on most of the dorsal face of the basihyal.

Summary. The cranes and the limpkin are quite distinct from the rallids in having the two muscles inseparably fused and in having an accessory part. In the rallids the two muscles are quite distinct from each other and are of different lengths. For minor variations, _Aramus_ and _Balearica_ show almost as many points of agreement as do _Balearica_ and _Grus_. _Aramus_ is unique in having these muscles insert on the entoglossum. The two muscles are apparently good familial indicators, since some unique differences occur in each family.

33. *M. tracheohyoideus*

Narrow and very elongate dermo-osseus muscle, compact in anterior and posterior regions but quite flattened in middle of belly. Forms part of wider sheet of muscle in posterior region of neck. Located on ventrolateral side of full length of neck, between trachea and skin. Attaches to larynx, to trachea, to skin, to *M. dermo-temporalis*, and to furculum.

Deep to *M. constrictor colli* throughout at least anterior two-thirds of neck. Adjacent to ventromedial edge of *M. tracheohyoideus* and fused with same in posterior half of neck.

Origin. Arises fleshily from most ventral edge of furculum, just lateral to mid-line. Originates as ventromedial portion of common sheet formed by its fusion with *M. dermo-temporalis*, but separates from ventral edge that muscle in about middle of length of neck.

Insertion. Inserts on skin throughout posterior half of length of belly, and attaches strongly to ventrolateral portion of trachea near anterior end. Main insertion (which might be considered as anterior origin) fleshy, mainly on posterolateral extent of cricoid, just posterior to insertion of *M. tracheohyoideus*. Small slip diverges near anterior end and further divides into smaller slips, some of which insert on ventrolateral portion of most anterior extent of trachea, and some of which attach to ventrolateral region of pharynx. Latter slips more or less continuous with portion of origin of *M. thyrohyoideus* in same area.

Action. Acts mainly with *M. dermo-temporalis* as flexor of skin of neck, but may also retract trachea.

Comparisons. In the Gruidae the muscle in Balearica (and Aramus) extends from the furculum to the larynx, but in Grus it occupies only the anterior third of the neck. In Balearica (and Aramus) it arises fleshily from the furculum, but in Grus it arises from the skin and from fascia between the trachea and the vertebral column, about 14 cm from the anterior end of the neck. In Balearica the muscle is considerably thinner than in Aramus; the comparison is not available for Grus. In Balearica the origin is from the full width of the anterior face of the ventromedial portion of the furculum (only from the ventromedial edge in Aramus), and the posterior portion of the belly is indefinably fused with M. dermo-temporalis (fused but still traceable in Aramus). In Grus the muscle is not present in this portion of the neck. In both cranes the muscle attaches to the anterior third of the trachea (only to the anterior end in Aramus). In Balearica (and Aramus) the main insertion is on the side of the posterior edge of the cricoid, but in Grus it is on the ventral, lateral, and dorsal surfaces of the posterior end of that cartilage. The cranes agree with Aramus in having a small, divergent slip form a portion of the insertion. This insertion is compact in the gruids, on the wall of the pharynx and the dorsal surface of the cricoid in Balearica, and on the arytenoid in Grus (in Aramus the slip diverges into a variable number of smaller ones that attach to the trachea and pharynx).

In the Rallidae the muscle in Rallus agrees with that of Aramus in dividing into a main portion and a small slip, but

in _Fulica_ it is not divided. In both rallids the origin from _M. dermo-temporalis_ is like that of _Aramus_. In _Rallus_ the main origin comes from the sternoclavicular ligament and the anteroventral corner of the keel of the sternum, ventral to the bundles of _M. dermo-temporalis_. In _Fulica_ it arises mainly from the sternoclavicular ligament, dorsal to the bundles of _M. dermo-temporalis_, but it soon crosses deep to that muscle to assume the usual position along the ventro-medial edge (in _Aramus_ this origin is from the furculum). In _Rallus_ (and in _Aramus_) it remains fused with _M. dermo-temporalis_ through its posterior half, but in _Fulica_ it is fused only at the origin. In _Rallus_ there is very little attachment to the trachea anteriorly, but in _Fulica_ (and _Aramus_) it attaches for about the anterior third of its length and has strong attachment to the dorsal side of the trachea for a distance of about one cm. In _Rallus_ (and _Aramus_) the main portion inserts on the side of the posterior end of the cricoid, and the small slip inserts on the dorsal side of the larynx (and also on the pharynx in _Aramus_). In _Fulica_ there is no division, and the anterior end of the muscle inserts as a single unit on the lateral and dorsal sides of the posterior edge of the larynx.

Summary. In _Grus_ the muscle is much shorter than in the other genera, and the condition corresponds well with that described by Fisher and Goodman (1955) for _M. dermo-temporalis_ in this crane. The reduction indicates a general decrease in the movability of the cervical skin in _Grus_.

Variations occur between the members of the Gruidae and the Rallidae in both posterior and anterior attachments. Aramus is unique in having the most anterior portion of the insertion divided into several small slips.

34. _M._ _tracheolaryngeus_ _superior_
35. _M._ _tracheolaryngeus_ _inferior_

Single, elongate band of muscle, wide and thin in anterior portion and more compactly narrow in posterior three-fourths. Posterior extent divided into two slips. Thinner portion covers ventral surfaces of larynx and anterior 2.5 cm of trachea. Narrower portion continues from that point along side of trachea to syrinx.

Fisher and Goodman (1955) found this muscle in two parts, _superior_ and _inferior_, which they described as separate muscles.

At anterior end medial edges of right and left sheets nearly in contact at mid-line. Lies deep to _M._ _constrictor_ _colli_ and _M._ _tracheohyoideus_ throughout most of length of neck. Posteriorly, two slips pass on either side of insertion of _M._ _sternotrachealis_.

Origin. Since this muscle does not attach to bone, and is attached to movable structures at both ends, it is not possible to designate a trenchant origin or insertion. It seems most reasonable to regard both the laryngeal and bronchial attachments as origins and the entire intervening tracheal attachment as the insertion; that interpretation is followed here.

Anterior origin (listed as insertion of _M_. _tracheolaryngeus superior_ in Fisher and Goodman, 1955, and origin of _M_. _tracheo-lateralis_ by Miskimen, 1951) arises from full length and most of width of cricoid cartilage of larynx. Posterior origin (comparable to insertion of _M_. _tracheolaryngeus inferior_ of Fisher and Goodman, and to insertion of _M_. _tracheo-lateralis_ in Miskimen) arises partly from most anterior syringeal cartilage. From this point muscle immediately divides into two slips that rejoin at another portion of origin, just anterior to insertion of _M_. _sternotrachealis_; one slip may give off tiny fasciculus to previous muscle.

Insertion. Wider anterior end attaches loosely to most of ventral surface of trachea, but soon narrows and moves laterad to insert loosely on narrow area along side of remainder of length of trachea.

Action. Shortens trachea by drawing together cartilaginous rings but probably also retracts larynx and protracts syrinx and bronchus.

Comparisons. The condition of the muscle in the limpkin is closely approached in some passerines, according to Miskimen's descriptions. However, she gives the laryngeal attachment as the origin and states that the muscle divides at its attachment to the anterior end of the syrinx to form _Mm_. _broncho-trachealis anticus_ and _posticus_, which insert on the anterior end of the bronchus. The latter two seem to represent separate muscles that are equivalent to the two slips of the posterior end of _M_. _tracheolaryngeus_ in _Aramus_.

In the Gruidae the muscle in _Balearica_ agrees with the single condition in _Aramus_, but in _Grus_ it is divided into _superior_ and _inferior_ parts, both of variable length. The inferior part in _Grus_ is narrower and much longer than the corresponding portion in _Balearica_ (or _Aramus_) because of the extra length of the coiled trachea. The anterior origin in _Balearica_ and _Grus_ is restricted to the medial portion of the ventral edge of the cricoid (in _Aramus_ it arises from most of the ventral surface and the full width of the posterior edge of the cartilage). In _Balearica_ the posterior origin is by a single tendinous band that extends anteriorly about halfway to the insertion of _M_. _sternotrachealis_ (as previously noted by Beddard, 1898). In _Grus_ this tendon is very short (in _Aramus_ the muscle arises, essentially fleshily, from the syrinx by two heads that eventually fuse). In _Balearica_ (and _Aramus_) the anterior portion of the muscle is wide and attached to the ventral surface of the trachea, but in _Grus_ this portion is narrower and apparently attached mainly at the posterior end of the _superior_ part. In the two cranes the muscle receives the insertion of _M_. _sternotrachealis_, but in _Aramus_ the muscle divides and passes on either side of the insertion of _M_. _sternotrachealis_.

In the Rallidae the muscle is somewhat larger than in _Aramus_. In _Fulica_ alone, it is very highly developed, forming a continuous sheet from the dorsal to the ventral midline in the anterior and posterior portions of the trachea. There is even some overlap of the muscles from the two sides

on the dorsal surface of the posterior portion of the trachea, and the muscle extends farther anteriorly on the side of the trachea than in _Rallus_ (or _Aramus_). In all three specimens of _Rallus_ the muscle on the left side divides posteriorly into three branches. The first of these continues posteriad to become the posterior origin, the second becomes the left _M. sternotrachealis_, and the third passes across the ventral surface of the trachea to emerge with the right _M. sternotrachealis_. The third branch is lacking on the right side in _Rallus_ and is absent on both sides in _Fulica_, although in the latter genus the muscles on the two sides are in contact by a thin ventral sheet (in _Aramus_ there is no contact between the muscles of the two sides, little or no contribution to _M. sternotrachealis_, and on each side the muscle divides into two heads, both of which continue to the posterior origin). In both rallids the anterior origin is from a smaller and more posterior portion of the ventral surface of the cricoid than in _Aramus_. The posterior origin is fleshy in both rallids (as in _Aramus_), but in _Fulica_ it is much wider. The insertion on the trachea is generally weaker in _Rallus_ than in _Fulica_ (or _Aramus_).

Summary. This muscle is somewhat variable among the three families and has intrafamilial differences in the Gruidae and Rallidae. _Aramus_ agrees with the rallids in having a fleshy posterior origin, compared with the tendinous one in the gruids. In the rallids the muscle gives off large branches to form _M. sternotrachealis_, but in the non-rallids

there is little or no contribution to that muscle. _Balearica_ is similar to _Fulica_ in the high degree of development of the muscle, but it is considerably greater in the latter genus. Unique specializations include the divided posterior end in _Aramus_, the complete separation into two distinct muscles in _Grus_, and the remarkable asymmetry in _Rallus_.

36. _M. sternotrachealis_

Small rounded muscle, about 1.5 mm in diameter and about 30 mm long. Located in lateral region of space anterior to heart. Connects trachea to rib cage, and also attaches to _M. obliquus abdominis externus_, to _M. scalenus_ and to _Mm. intercostales externi_.

Proximal end deep to anterior edge of _M. obliquus abdominis externus_. Distal end contacts _M. tracheolaryngeus_. Proximal end lies superficial to a small posterodorsal portion of deep part of _M. sternocoracoideus_.

Origin. Arises by wide aponeurosis from ventral centimeter of last cervical rib and from upper third of first sternal rib. Attaches also to portions of _M. scalenus_, _M. obliquus abdominis externus_, and most anterior of _Mm. intercostales externi_. Aponeurosis narrows abruptly, becomes fleshy, and soon changes into rounded belly.

Insertion. Attaches to side of posterior end of trachea, between the two slips of _M. tracheolaryngeus_, just posterior to their point of origin.

Action. Retracts trachea, lengthening it and decreasing tension on syrinx (see Miskimen, 1951).

Comparisons. In the Gruidae the muscle in Balearica originates, less extensively than in Aramus, from the angle between the sternal and vertebral parts of the first true rib, but in Grus the origin is from the sternocoracoidal process of the sternum. These two locations of the origin in the gruids were described by Beddard (1898). In both cranes the muscle inserts directly on M. tracheolaryngeus (inserts between the two slips of that muscle in Aramus).

In the Rallidae the origin resembles that of Aramus, but is somewhat more extensive on the left side. In both rallids the muscle inserts as a branch of M. tracheolaryngeus (see the description of that muscle). In Rallus the right muscle divides and contributes to M. tracheolaryngeus on both sides, but the left muscle is unbranched in Rallus, and both sides are unbranched in Fulica (in Aramus both sides are unbranched and have little connection to M. tracheolaryngeus). In both rallids the insertion of the muscle on the right side is slightly posterior to the left insertion (in Aramus the insertions are symmetrical).

Summary. In Aramus the muscle has very little connection to M. tracheolaryngeus, but there is more in the Gruidae, and in the Rallidae the two muscles are continuous with each other. Grus is distinct from Balearica and the non-gruids in having the origin from the sternum. The rallids are unique in having both the origin and the insertion asymmetrical.

37. _M_. _thyroarytenoideus_

Small and flattened triangular muscle. Located on posterolateral portion of larynx. Attaches to cricoid and to arytenoid cartilages.

Anterolateral edge adjacent to portion of origin of _M_. _thyrohyoideus_ arising from larynx. Posterolateral corner of belly ventral to insertion of portion of small slip of _M_. _tracheohyoideus_. Superficial, in dorsal view of larynx, to _M_. _constrictor_ _glottidis_.

Origin. Arises fleshily from posterior edge of cricoid and dorsal side of posterolateral portion of lateral cricoid.

Insertion. Inserts fleshily on lateral edge of arytenoid cartilage.

Action. Opens glottis by moving arytenoid laterad.

Summary. The pattern of this muscle is the same in all the genera studied in the three families.

38. _M_. _constrictor_ _glottidis_

Small and flattened, triangular muscle. Located on dorsal side of larynx. Attaches to medial and lateral cricoids and to arytenoid.

Deep in dorsal view to _M_. _thyroarytenoideus_. Anterolateral edge adjacent to portion of origin of _M_. _thyrohyoideus_ arising from larynx.

Origin. Originates fleshily from medial cricoid and from dorsal surface of lateral flange on posterior half of arytenoid.

Insertion. On medial side of anterior half of lateral cricoid.

Action. Closes glottis.

Comparisons. In the Gruidae the portion of the origin from the lateral flange of the arytenoid is lacking in *Grus* (as in *Aramus*), and the insertion is on connective tissue around the anterior end of the arytenoid as well as on the lateral cricoid (only on the lateral cricoid in *Aramus*).

This muscle was not found in *Balearica*, but the region was not well preserved. The muscle is presumably present in a reduced condition in this crane.

In the Rallidae the muscle in *Rallus* arises only from the medial cricoid (arises also from the lateral flange of the arytenoid in *Aramus*), but in *Fulica* it arises from the medial cricoid and all along the side of the arytenoid cartilage. In *Rallus* the insertion is partly on connective tissue around the anterior end of the arytenoid and partly on the middle of the dorsomedial rim of the lateral cricoid cartilage (in *Aramus* the insertion is only on the anterior half of the lateral cricoid). In *Fulica* the insertion is only on the lateral cricoid, but it occupies the entire dorsomedial edge.

Summary. Some rearrangement of the muscle has apparently occurred in the evolution of the various genera. In *Aramus*, and even more so in *Fulica*, the origin is moved anteriorly onto the arytenoid. This attachment may be associated with a need for more effective closing of the glottis in these two

underwater feeders. The muscle is essentially the same in Grus and Rallus. Its presence is uncertain in Balearica.

Muscles of the Orbit

39. M. orbicularis palpebrarum

This muscle sheet is greatly reduced in the limpkin, and is represented by only a few fibers on the inner side of the lower lid. Its action (Shufeldt, 1890) is to close the eye, mainly by raising the lower lid.

Comparisons. In the Gruidae it is apparently better developed in Grus, arising from the anterior end of the jugal bar and from the lacrimal bone and inserting mainly on the lower eyelid. Only a few fibers of the muscle could be found in Balearica, perhaps partly because of inadequate preservation in the region.

In the Rallidae no trace of the muscle was found.

Summary. The muscle exists as a recognizable sheet only in Grus. It is much reduced in the other genera and is probably absent in Rallidae.

40. M. levator palpebrae superioris

Very thin, wide sheet with few contractile fibers. Covers upper side of eyeball. Attaches to roof of orbit and to upper lid.

Encloses dorsal side of eyeball and eye muscles on that surface.

Origin. Arises from inner edge of roof of orbit.

Insertion. Inserts into inner side of upper lid.

Action. Helps open eye by raising upper lid.

Summary. The muscle is the same in the limpkin, the two cranes, and both rallids.

41. _M. depressor palpebrae inferioris_

Very thin, wide sheet with few contractile fibers. Covers posteroventral region of eyeball. Attaches to interorbital septum and to lower lid.

Superficial to _M. rectus externus_ and _M. rectus inferior_.

Origin. Arises from ventral region of interorbital septum, along narrow line just ventral to origins of _M. rectus inferior_ and _M. rectus externus_.

Insertion. Fuses to inner side of most of length of lower lid.

Action. Opens sye by depressing lower lid.

Comparisons. In the Gruidae it arises from a very small area just dorsal to the anterior end of the origin of the _M. protractor quadratus_ (the area of origin is very elongate in _Aramus_ and located just ventral to the origins of the lower two rectus muscles).

In the Rallidae the muscle in _Rallus_ is essentially like that of _Aramus_, but in _Fulica_ the line of origin is longer and extends farther anteriorly.

Summary. The origin of the muscle in the two cranes is small and located posteroventral to the elongate origin of _Aramus_ and the two rallids. Otherwise the muscle is similar in all three families.

42. _M_. _quadratus_ _nictitantis_

Thin, somewhat rhomboidal sheet with bundles converging to smaller ventral edge. Visibly separate in upper region into smaller anterior and larger posterior portions. Lies over most of dorsal region of inner side of eyeball. Attaches to sclera and to tendon of _M_. _pyramidalis_ _nictitantis_.

In medial view of eye, lies partly deep to _M_. _obliquus_ _superior_, to _M_. _rectus_ _superior_, and to _M_. _rectus_ _externus_. Fascia of ventral edge encloses small tendon of _M_. _pyramidalis_ _nictitantis_.

Origin. Arises from thin longitudinal line extending about one-third of circumference of eyeball, along its dorsomedial aspect.

Insertion. Inserts as fascial pulley enclosing tendon of _M_. _pyramidalis_ _nictitantis_.

Action. Maintains tension on enclosed tendon, to hold it away from optic nerve and to allow it to move nictitating membrane.

Comparisons. In the Gruidae the muscle in _Balearica_ (as in _Aramus_) is large, with a partial division in the upper region, but in _Grus_ the belly is considerably smaller and apparently has no division.

In the Rallidae _Rallus_ has a smaller belly with less of it covered by _M_. _rectus_ _superior_ than in _Fulica_ (or _Aramus_), and the pulley is likewise smaller. In _Rallus_ the pulley enclosing the tendon of _M_. _pyramidalis_ _nictitantis_ is shorter than in _Fulica_ (or _Aramus_).

Summary. This muscle is generally similar in all the genera examined, but some minor variations seem to have arisen as adaptations. The belly is larger in _Aramus_, _Balearica_, and _Fulica_ than in _Grus_ and _Rallus_, implying more use of the nictitating membrane in the first three than in the latter two. This may be related to the more aquatic habitat, at least of _Aramus_ and _Fulica_. A definite partial division in the belly is present in each genus except _Grus_, but the separation is quite small in _Rallus_. The significance of this is not clear, but it seems to correlate well with the differences in size.

43. _M_. _pyramidalis_ _nictitantis_

Composed of small, flat, and elongately triangular belly with very slender, rounded tendon leading from apex. Located on anteroventral region of inner side of eyeball, just anterodorsal to optic nerve. Tendon extends around to posteroventral region of lateral surface of eyeball. Attaches to sclera, to _M_. _quadratus_ _nictitantis_, and to nictitating membrane.

In medial view partly deep to _M_. _obliquus_ _inferior_, to _M_. _rectus_ _inferior_, and to _M_. _rectus_ _internus_. Inserting tendon passes through pulley formed by free end of _M_. _quadratus_ _nictitantis_.

Origin. Arises from narrow longitudinal line of sclera at anteroventral edge of inner side of eyeball.

Insertion. Small tendon leaves apex of belly, passes through pulley of _M_. _quadratus_ _nictitantis_, and passes to

ventrolateral region of eyeball to insert on posteroventral corner of nictitating membrane.

Action. Pulls nictitating membrane posteriad, covering cornea.

Comparisons. In the Gruidae the muscle is similar to that of *Aramus* but it seems to be slightly smaller in *Grus* than in *Balearica* (and *Aramus*).

In the Rallidae the muscle in *Rallus* is larger than in *Fulica* (and considerably larger than in *Aramus*), and a smaller portion is enclosed by the pulley of *M. quadratus nictitantis* than in *Fulica* (or *Aramus*).

Summary. The muscle varies only in size among the genera studied, but the differences occur within the Gruidae as well as within the Rallidae. The larger size of this muscle in *Rallus* is contrasted with the smaller size of *M. quadratus nictitantis* in that genus. It would seem, on the basis of the present muscle, that *Rallus* has more use of the nictitating membrane, but the smaller size of the former muscle indicates that such an interpretation is oversimplified.

44. *M. obliquus superior*

Flat and fan-shaped. Lies on anterodorsal surface of inner side of eyeball. Attaches to interorbital septum and to sclera of eyeball.

Deep to *M. levator palpebrae superioris*, and posterolateral edge deep to *M. rectus superior*. Superficial to anterodorsal edge of *M. quadratus nictitantis*.

Origin. Arises fleshily from elongately oval scar at extreme anterodorsal extent of interorbital septum.

Insertion. Inserts by short but wide aponeurosis, onto sclera of posterodorsal region of inner side of eyeball, mostly between origin of _M. quadratus nictitantis_ and insertion of _M. rectus superior_.

Action. Rolls eyeball inward in anterodorsal direction.

Comparisons. In the Gruidae the proximal end and its area of origin are large (relatively small in _Aramus_). In _Balearica_ (and _Aramus_) the insertion is wider than in _Grus_.

In the Rallidae the elongate area of origin in _Rallus_ is oriented nearly vertically but is more nearly horizontal in _Fulica_ (and _Aramus_). In _Rallus_ the belly is fleshy to the point of insertion, but there is a short aponeurosis in _Fulica_ (and a more extensive one in _Aramus_).

Summary. Only very slight differences exist in this muscle among the genera, but some occur within the Gruidae and Rallidae. The two cranes differ from _Aramus_ and the two rallids in having a considerably larger area of origin for this muscle.

45. _M. obliquus inferior_

Narrow and partially rounded band of muscle. Located on anteroventral portion of inner side of eyeball. Attaches to interorbital septum and to sclera.

Superficial to anterior edge of _M. pyramidalis nictitantis_ and to anterior edge of _M. rectus internus_.

Origin. Arises fleshily from rounded scar in middle of extreme anterior edge of interorbital septum.

Insertion. Attaches by short aponeurosis to sclera in anteroventral region of inner side of eyeball.

Action. Rotates eyeball in anteroventral direction.

Comparisons. In the Gruidae the muscle is widely flattened (narrow and rounded in *Aramus*). In *Balearica* (and *Aramus*) it originates from the middle of the anterior edge of the interorbital septum. Fisher and Goodman (1955) show this origin (p. 11) as arising with the rectus muscles from a scar just anteroventral to the optic foramen. Apparently the drawing is incorrect in this point, since they state (p. 37) that the eye muscles follow the usual vertebrate pattern; furthermore, skeletons examined of *Grus grus*, *G. canadensis*, *Anthropoides paradisea*, and *A. virgo* all plainly show a scar in the location described above for *Balearica* and *Aramus*.

In the Rallidae the area of origin in *Rallus* (and *Aramus*) is rounded, but it is elongate in *Fulica* and closer to the origin of the other oblique muscles.

Summary. This muscle is similar in all genera dissected, except perhaps *Grus* (see above).

46. *M. rectus superior*

Flat and elongately triangular muscle. Lies over posterodorsal aspect of inner side of eyeball. Attaches to interorbital septum and to sclera.

Deep to *M. levator palpebrae superioris*. Superficial to posterolateral corner of *M. obliquus superior* and to potion of *M. quadratus nictitantis*.

Origin. Originates fleshily from oval scar on posterodorsal edge of interorbital septum.

Insertion. Belly changes to thin aponeurosis in upper third and inserts on narrow line on sclera in dorsal region of inner side of eyeball, along dorsal edge of insertion of *M. obliquus superior*.

Action. Rotates eyeball anterodorsad.

Comparisons. In the Gruidae the muscle is essentially the same as in the limpkin.

In the Rallidae the muscle in *Rallus* differs from that of *Aramus* only in arising from an area slightly closer to the optic foramen. The origin in *Fulica* is located intermediate to that of *Rallus* and *Aramus*.

Summary. The muscle is quite similar in all genera studied.

47. *M. rectus inferior*

Small band of muscle. Located on posteroventral region of inner side of eyeball. Attaches to interorbital septum and to sclera.

Superficial to ventral edge of *M. pyramidalis nictitantis*.

Origin. Arises fleshily from oval scar on interorbital septum, just anteroventral to optic nerve.

Insertion. Becomes aponeurotic in ventral 3 mm and inserts on anteroventral region of inner side of eyeball.

Action. Rotates eyeball anteroventrad.

Comparisons. In the Gruidae the area of origin is posteroventral to the optic foramen (anteroventral to that foramen in *Aramus*).

In the Rallidae the muscle differs from that of the limpkin only in being slightly more rounded.

Summary. The two cranes differ slightly from Aramus and the rallids in the location of the origin, but the rails differ from Aramus and the cranes in having the belly slightly more rounded. Other features are closely similar in all three families.

48. M. rectus externus

Short, moderately thick band of muscle. Lies on posteroventral region of inner side of eyeball. Attaches to wall of orbit and to sclera.

Superficial to portion of tendon of M. pyramidalis nictitantis.

Origin. Arises fleshily from rounded scar, which partially surrounds foramen for sixth cranial nerve, on wall of orbit just posteroventral to optic foramen.

Insertion. Attaches by thin, short aponeurosis to sclera of posterior region of inner side of eyeball.

Action. Rotates eyeball posteriad.

Comparisons. In the Gruidae the area of origin in Balearica is posterior to the optic foramen, but in Grus it is posterodorsal to the foramen (posteroventral to it in Aramus). The muscle is otherwise similar in the two cranes and the limpkin.

In the Rallidae the area of origin is wide and adjacent to the posterior edge of the optic foramen (narrower in Aramus and posteroventral to the optic foramen).

<u>Summary</u>. The muscle differs among the three families only slightly in the position of the origin, which arises from a slightly different location in each family.

49. <u>M</u>. <u>rectus</u> <u>internus</u>

Relatively wide band of muscle. Located in middle and anterior regions of inner surface of eyeball. Attaches to interorbital septum and to sclera.

Superficial in medial view to ventral edge of belly of <u>M</u>. <u>quadratus</u> <u>nictitantis</u> and to dorsal end of belly of <u>M</u>. <u>pyramidalis</u> <u>nictitantis</u>.

<u>Origin</u>. Arises fleshily from interorbital septum, partly from bone and partly from connective tissue closing interorbital foramen.

<u>Insertion</u>. Attaches by thin aponeurosis, about 4 mm long, onto sclera of anterior region of inner surface of eyeball.

<u>Action</u>. Rotates eyeball anteriad.

<u>Comparisons</u>. In the Gruidae the origin in <u>Balearica</u> (and <u>Aramus</u>) is wide and located anterior and anterodorsal to the optic foramen, but in <u>Grus</u> it is rounded and located anterior to the optic foramen.

In the Rallidae the muscle and its origin are wider than in <u>Aramus</u>, but it is otherwise quite similar in all three genera.

<u>Summary</u>. Among the three families the muscle differs only in being slightly wider, with a wider origin, in Rallidae than in Aramidae and Gruidae.

50. M. tensor tympani

This muscle could not be found in any of the genera used in this study, and Fisher and Goodman likewise did not find it in their dissections. If such a muscle is present in these gruiforms, it must be highly reduced.

Muscles of the Wing

51. M. tensor patagii longus

Complex association of two main elastic tendons, a very thin and extensive inelastic sheet, and one small belly (the biceps slip; see Berger, 1956a). Lies within patagium. Attaches to M. patagii brevis, to M. biceps, to M. extensor metacarpi radialis, to M. pectoralis, to fascia of forearm, carpus, radius, and manus, and to metacarpal II.

Main inserting tendon superficial at wrist to M. abductor alae digiti II and to inserting tendons of M. extensor metacarpi radialis and M. extensor longus digiti II.

Origin. Arises mainly as fascial continuation of proximal end of belly of M. tensor patagii brevis, partly by strong fascial sheet (pars patagialis of Berger, 1956a), 7 mm wide, arising from M. pectoralis, near proximal extent of its attachment to deltoid crest. Originates also by thin, fleshy slip from M. biceps, near distal edge of deltoid crest.

Mitchell (1915) and Berger (1956a) refer to the belly of the muscle, considered here as M. tensor patagii brevis, as the combined bellies of the longus and the brevis.

Insertion. Inserts mainly by long, attenuate tendon, continuous with both elastic tendons, which passes over

anterior side of wrist and attaches onto distal and ventral portion of extensor process of metacarpal II between two parts of _M. abductor alae digiti_ II, to fascial sheets covering both sides of manus, and indirectly to _M. flexor digiti_ II. Thin sheet extends from full length of elastic tendons to insert on distal tendon of _M. tensor patagii brevis_, on belly of anconal part of _M. extensor metacarpi radialis_, on fascia of radius, and on fascia along posterodorsal edge of forearm. This is the forearm anchor of Mitchell (1901).

Action. Tenses anterior edge of patagium and extends hand.

Comparisons. In the Gruidae the fleshy origins from _M. tensor patagii brevis_ and _M. biceps_ are similar to those of _Aramus_. In the cranes the common tendon of the _longus_ and _brevis_ (Mitchell, 1901) extends for about 2 cm, but is shorter in _Aramus_. In _Balearica_ the origin from _M. pectoralis_ extends along the entire anteroventral edge of the belly of _M. tensor patagii brevis_ and onto the proximal end of the _longus_ tendon, but this origin is narrow (2 cm) in _G. canadensis_ (and _Aramus_) and is associated only with _M. tensor patagii brevis_) in _G. americana_. In _Balearica_, _G. americana_, and apparently in _G. canadensis_, an elastic tendon from the deltoid crest contributes to the origin, but in _Aramus_ this tendon contributes only to the _brevis_. The main insertion on the extensor process is largely similar in the cranes and _Aramus_, and the indirect fascial connection to the alular muscles is absent only in _G. americana_. The insertion of the

thin sheet onto the elbow in *Balearica* differs from that of *Aramus* by attaching first to patagial skin. In *G. americana* this insertion is accomplished by six small and inelastic tendons, but the attachment is entirely absent in *G. canadensis*. In *Balearica* the forearm anchor is very much thinner than in *Aramus* and is apparently lacking in *Grus*. Uniquely in *Balearica* a third inelastic branch diverges at the level of the origin of from *M. biceps* and soon merges gradually with the skin of the patagium.

In the Rallidae the two muscular origins are similar to those of *Aramus*, but in *Fulica* the origin from *M. biceps* differs from that of *Rallus* (and *Aramus*) in contributing also to *M. tensor patagii brevis*. In *Rallus* the common tendon is even shorter than in *Aramus*, but in *Fulica* it is several millimeters long. In *Rallus* a single small tendon comes from the deltoid crest, but the corresponding tendon in *Aramus* contributes only to *M. tensor patagii brevis*. In *Fulica* a similar tendon arises from the deltoid crest, but another comes from the humerus just distal to the crest, and both contribute to both the *longus* and the *brevis*. In *Rallus* the tendinous slip from *M. pectoralis* is very small, but it is wider (3 mm) in *Fulica* (and *Aramus*). In both rallids the muscle divides into four elastic tendons (into two in *Aramus*) within the patagium, and three of these recombine to insert on the anterior side of the distal end of the radius, while the other inserts on fascia over the manus and on a connective pad lying between the distal end of the radius and the

extensor process of metacarpal II (only one insertion is present in Aramus, on the extensor process and surrounding fascia).

Summary. The complicated origin has only minor variations in the genera studied. The inserting ten n has a remarkably specialized complexity in G. americana but is rather simple in Balearica, G. canadensis, and the non-gruids. The two main divisions of the elastic tendon in the limpkin and the cranes differ from the four-parted condition in the two rallids. The most distinctive difference is the single insertion at the wrist in Aramus and the gruids, contrasted with the double insertion of the rallids.

52. M. tensor patagii brevis

Flat band of muscle, fleshy and 9 mm wide in proximal two-fifths, tendinous and averaging 6 mm wide in distal three-fifths. Lies over dorsal side of humeral portion of wing. Attaches to furculum, to deltoid crest of humerus, to M. tensor patagii longus, to M. extensor metacarpi radialis, and to fascia over elbow and posterior edge of forearm.

Proximal end adjacent to cervical part of M. cucullaris. Posterior end attached to proximal portions of tendons of M. tensor patagii longus. Proximal end superficial to portions of M. deltoideus major, M. coracobrachialis anterior, and M. deltoideus minor. Distal end dorsal to proximal end of M. extensor metacarpi radialis.

Origin. Arises fleshily and tendinously from facet on dorsal face of dorsal end of furculum. Somewhat attached to insertion of axillary part of M. cucullaris, on portion

lying between latter insertion and origins of *M. deltoideus major* and *M. coracobrachialis anterior*. Arises also by small inelastic tendon from deltoid crest of humerus.

Insertion. Tendon gives rise to tendons of *M. tensor patagii longus* and becomes gradually wider. Finally inserts on *M. extensor metacarpi radialis* by two incompletely divided slips, one on belly of palmar part, and another on tendon of origin of anconal part. The latter seems to correspond to the distal slip of Mitchell (1901). Former tendon also merges with strong fascia that attaches to distal end of humerus, to common tendon of *M. extensor digitorum communis* and *M. supinator brevis*, and to *M. flexor metacarpi radialis* in region of elbow. This tendon then extends along postero-dorsal edge of forearm, attaches to distal half of radius, merges with fascia over wrist and manus, and attaches to bases of eathers along ulna. The latter attachment corresponds to medial slip of Mitchell (1901).

Action. Acts with *M. tensor patagii longus* in tensing patagium and extending hand. Also aids in flexing elbow and contributes to airfoil contour of wing.

Comparisons. In the Gruidae the main origin in *Balearica* is only slightly different from that of *Aramus*, arising from the dorsomedial face of the dorsal end of the furculum. In *Grus* it arises from the lateral face of the same end of that bone, but in *G. canadensis* an additional component comes from the acromion of the scapula. In *Balearica* (but not in *Aramus*) the entire ventromedial edge is attached tendinously to

M. pectoralis, but this origin is much smaller in both species of Grus. In Balearica only, the posterodorsal edge of the belly is closely connected by fascia to M. deltoideus major. The tendinous origin from the deltoid crest is apparently present in all, but only in Balearica (and Aramus) is it associated only with the brevis. In Balearica the insertion differs from that of Aramus in lacking even the partial division (Lowe, 1931), and it is usually undivided in the two species of Grus. It inserts on M. extensor metacarpi radialis in all three cranes (and Aramus) but attaches to M. flexor carpi ulnaris only in G. americana. In Balearica (and Aramus), but not in Grus, the inserting tendon is joined by a portion of the longus tendon.

In the Rallidae the main origin in Rallus is from the furculum, but in Fulica it also arises from the acromion of the scapula. In Rallus the origin from the biceps is absent, although some fascial connection persists. In Fulica some origin from the biceps slip is present, but the slip also contributes to the longus (connects only to the longus in Aramus). The small tendon of origin from the deltoid crest is similar in the rallids and in Aramus, but in Fulica a second tendon originates from the humerus just distal to the crest. The inserting tendon in Rallus is slightly more divided than in Aramus, but it is undivided in Fulica. The points of insertion in both rallids are quite similar to those of Aramus, but the sheet over the elbow and forearm is weaker in Rallus.

Summary. This muscle varies only in what seem to be insignificant points in the genera examined. The main variation is in the presence or absence of a division in the inserting tendon, but this characteristic differs within the families, even within one species. The overall constancy of the muscle indicates that it has been very conservative in the evolution of the group.

53. M. pectoralis

Very large muscle, partially divided anterodorsally into superficial and deep portions. Comprises major portion of breast musculature. Attaches to M. obliquus abdominis externus, to sternum, and xiphoid cartilage, to M. supracoracoideus, to furculum, to coracoid, to M. coracobrachialis anterior, to M. biceps, to humerus, and to M. tensor patagii longus.

Fisher and Goodman (1955) found this muscle in the whooping crane to be completely divided into superficial and deep parts. In the limpkin this separation is quite evident in most of the anterodorsal region, but the two parts are inseparably fused at the insertion and in the posterior third of the belly.

Superficial to anteroventral half of M. obliquus abdominis externus, to M. supracoracoideus, to M. coracobrachialis posterior, to M. coracobrachialis anterior, and to anterior end of origin of M. biceps.

Origin. Extensive and mostly fleshy. Arises very loosely from most of ventral half of M. obliquus abdominis

externus, from xiphoid cartilage, from portions of plate and side of keel of sternum not occupied by _M_. _supracoracoideus_, very loosely from ventral surface of latter muscle, and from dorsal and dorsolateral faces of all but anterodorsal tip of furculum. The last origin loosely contacts furcular attachments of _M_. _dermo-temporalis_ and _M_. _tracheohyoideus_.

Insertion. Main attachment mostly fleshy, but with heavily tendinous inner border, on palmar side of all but proximal portion of deltoid crest of humerus. Also inserts tendinously on proximal end of _M_. _biceps_, on distal end of _M_. _coracobrachialis_ _anterior_, on dorsolateral corner of extreme anterior tip of coracoid, and on coracohumeral joint capsule. Also has one strong tendinous band of attachment to skin, near anterodorsal end of belly, and small tendinous insertion, previously described, on _M_. _tensor_ _patagii_ _longus_.

Action. Provides main power for downstroke of wing.

Comparisons. In the Gruidae the muscle undergoes change. The one specimen of _Balearica_ and at least some specimens of _G_. _canadensis_ (Fisher and Goodman, 1955) agree with _Aramus_ in having the muscle incompletely divided, but in _G_. _americana_, and according to Beddard (1898) in _Balearica_ _pavonina_, it is composed of two distinct parts. The main points of origin are comparable in all three cranes to those of _Aramus_, but in _Balearica_ (and _Aramus_), and perhaps in _G_. _canadensis_, the area of origin from the sternum extends beyond the posterior edge of the plate, onto the xiphoid cartilage. In _G_. _americana_ the origin does not extend quite to the posterior edge

of the sternal plate. In _Balearica_ (and _Aramus_) the furcular portion of the origin contacts the posterior ends of _M. dermo-temporalis_ and _M. tracheohyoideus_, but this contact is lacking in _G. americana_ and is unknown for _G. canadensis_. In _G. americana_ only, the main insertion is somewhat more complex and serves as the insertion of only the superficial part. _Balearica_ differs from _Aramus_ in lacking even the small attachment to _M. biceps_, but in both species of _Grus_ the muscle inserts very strongly onto the proximal end of that muscle, although this attachment is only for the deep part in _G. americana_. In _Balearica_ the insertion on the distal end of _M. coracobrachialis anterior_ is much weaker than in _Aramus_, and is lacking in _Grus_. The attachment to the capsule of the shoulder joint is similar in _Balearica_ and _Aramus_, but the attachment to the dorsal tip of the coracoid is more indirect in _Balearica_. In _Balearica_ the attachment to the skin, across the side of the dorsolateral portion of the belly, is much wider than in _Aramus_, but this connection is not mentioned for _Grus_. The attachment to the patagial tensor muscles is associated with only the _brevis_ in _Balearica_ and _G. americana_ (with only the _longus_ in _Aramus_) and with both _longus_ and _brevis_ in _G. canadensis_. In _G. americana_ only, the separate deep part has the specialized function of bracing the coracoid.

In the Rallidae, _Rallus_ is unique in lacking even the incomplete division of the main muscle. The major origin is similar in both rallids to that of _Aramus_, but some of the

more posterior portions differ in arising from fascia between the parts of the dissected sternum. In Rallus (and Aramus) the attachment of the muscle to M. dermo-temporalis and M. tracheohyoideus is more extensive and more direct than in Fulica. The main insertion in Rallus differs from that of Aramus in having an additional small tendon inserting on the lateral edge of the bicipital crest, and in Fulica a much larger one is present. Fulica alone has additional tendinous connections to M. biceps in this area. In Rallus the attachment to M. coracobrachialis anterior is smaller than in Fulica (and Aramus). Rallus differs from Aramus in having no connection of the muscle to the joint capsule or to the coracoid, but in Fulica an indirect one to the coracoid is present. In Rallus the tendon to the patagial muscles is much smaller than in Fulica (and Aramus). Both rallids differ strikingly from Aramus in having a separate dermal muscle, apparently a derivative of M. pectoralis, that arises from the distal end of the deltoid crest at the distal end of the insertion of M. pectoralis and inserts on the skin. This slip seems to be equivalent to M. pectoralis abdominalis, described in the Corvidae by Hudson and Lanzillotti (1955).

Summary. The overall configuration of this large muscle is rather similar in all genera examined, however, the rallids are distinct from the non-rallid in two points. In the Rallidae a strong portion of the insertion is on the bicipital crest, but this attachment is lacking in Aramidae and Gruidae. In the two rallids a separate dermal muscle,

apparently a derivative of *M. pectoralis*, adjoins the distal edge of the humeral attachment, but this dermal muscle is not found in the non-rallids. Other points of difference are minor and are variable within the families, but *Balearica* has more of these points in agreement with *Aramus* than with *Grus*.

54. *M. supracoracoideus*

Large and elongately triangular muscle, with strong tendon leading from anterior apex of bipinnate and somewhat flattened belly. Very small, partially separate portion connects to tendon anteriorly. Belly lies in anteromedial region of breast, but tendon extends through triosseal canal. Attaches to sternum, to *M. pectoralis*, to sterno-coraco-clavicular membrane, to coracoid, to *M. coracobrachialis posterior*, and to humerus.

Belly lies entirely deep to *M. pectoralis*. Adjacent to posteroventral edge of *M. coracobrachialis posterior*. Insertion of anterior part deep to *M. deltoideus minor* and connected to its insertion.

Origin. Arises from large triangular area of sternum, fleshily from anteromedial half of plate and tendinously from anterior surface and dorsal two-thirds of side of keel, except at posterior end. Also arises tendinously from single ventral sheet of sterno-coraco-clavicular membrane (Woolfenden, 1961), fleshily from remainder of that membrane, and fleshily from ventral and medial surfaces of shaft of coracoid. Small anterior portion arises separately from entire inner face of procoracoid process and from section of

sterno-coraco-clavicular membrane just ventral to process. Connected to *M. coracobrachialis posterior* along lateral edge of coracoid.

Insertion. Main insertion by strong, rounded tendon attaching to proximal face of external tuberosity of humerus. This tendon ossified at proximal end but not at insertion. Small fleshy portion lies on, and attaches to, superficial face of main tendon but extends to proximal edge of deltoid crest and attaches partly in common with insertion of *M. deltoideus minor*.

Action. Furnishes power for upstroke of wing by drawing humerus upward and anteriad.

Comparisons. In the Gruidae a heavy aponeurosis takes the place of the very thin sheet of connective tissue that separates this muscle from *M. pectoralis* in *Aramus*. In *Balearica* the small anterior portion agrees with that of *Aramus* in arising from the inside of the procoracoid and from the sterno-coraco-clavicular membrane, but in *Grus* it originates from the medial edge of the coracoid and from the furculum. This part is slightly larger than in *Grus* and is unique in extending all the way to the humeral insertion, even though its primary insertion is also on the main tendon. The origin of the main part in *Grus* has some minor specializations because of the sternal enclosure of the trachea. In *Balearica*, and apparently in *Grus*, the inserting tendon differs from that of *Aramus* in lacking ossification. In *Balearica* (and *Aramus*) the inserting tendon is entirely single, but it arises from the belly by two branches in *Grus*.

In the Rallidae the anterior portion is mostly fused to the main portion and ends distally on the main tendon in the triosseal canal (in _Aramus_ the anterior portion arises separately and extends to the distal end of the main tendon). No ossification occurs in the tendon in either rallid, nor in _Aramus_. In both _Rallus_ and _Fulica_ the main tendon is attached to most of the underside of _M_. _deltoideus_ _minor_ (in _Aramus_ the two muscles are connected only at their insertion).

Summary. Aramus agrees with Gruidae in having a partially separate anterior portion, but in Rallidae the two portions are fused. In Rallidae the inserting tendon is widely connected to _M_. _deltoideus_ _minor_, but there is only a small connection in Aramidae and none in Gruidae. _Grus_ is specialized in having a double derivation of the main tendon within the belly, and the ossification of the inserting tendon is apparently unique in _Aramus_. In all three gruids a heavy fascial sheet, not present in the other two families, separates this muscle from _M_. _pectoralis_. In some very minor features _Balearica_ is more like _Aramus_ than like _Grus_.

55. _M_. _sternocoracoideus_

Small muscle composed of three separate and flattened parts, superficial, intermediate, and deep. Located between and just posterior to sternocoracoidal processes of sternum and coracoid. Attaches to first two, and sometimes three, sternal ribs and to sternum and coracoid.

Fisher and Goodman (1955) also listed this muscle as "tripartite," but their dorsal fasciculus seems to include both the superficial and deep parts listed here.

Posterior portions deep to anteroventral portion of _M_. _obliquus_ _abdominis_ _externus_. Anterolateral edge of intermediate part deep to _M_. _coracobrachialis_ _posterior_. Posterior portions superficial to anteroventral extent of _Mm_. _intercostales_.

Origin. Superficial part arises fleshily and tendinously from anterolateral and posterolateral edges of sternal half of second sternal rib, sometimes from anterolateral edge of third sternal rib, and from anterior edge of ventral portion of first sternal rib. Intermediate part originates from anterolateral and anterodorsal edges of sternocoracoidal process of sternum. Deep part originates, dorsal to origin of superficial part, from anterior face of first sternal rib.

Insertion. Superficial part has mixed insertion on entire posterodorsal and anterolateral edges of sternocoracoidal processes of coracoid. Intermediate part inserts fleshily and tendinously on all of sternocoracoidal impression on dorsal side of coracoid. Deep part has mixed insertion on posterolateral tip of sternocoracoidal process of sternum.

Action. Apparently acts to brace coracoid, but may also act to slide base of coracoid laterad in coracoidal groove.

Comparisons. In the Gruidae the information is incomplete because in the one specimen of _Balearica_ the muscle on both sides was too badly damaged to be used in this study. In both species of _Grus_ the muscle includes all parts described for _Aramus_, but apparently the superficial and deep

parts are combined (separate in *Aramus*). The anterior bundle in *Grus* seems to correspond to the intermediate part in *Aramus*. In *Grus* the origin from the third sternal rib is constant (not always present in *Aramus*). The insertion on the anterolateral edge of the sternocoracoidal process of *Aramus* is not represented in *Grus*.

In the Rallidae, *Rallus* has the portions corresponding to the superficial and deep parts united (all parts are separate in *Aramus*), and in *Fulica* all three parts are somewhat joined. Areas of origin are similar in both rallids to those of *Aramus*. The most important insertion of the superficial and deep parts in *Rallus* is on the lateral tip of the sternocoracoidal process of the sternum, but in *Fulica* it is on the anterolateral edge of the sternocoracoidal process of the coracoid (in *Aramus* this insertion is about equally distributed between the posterior edges of the sternocoracoidal processes of the coracoid and the sternum). In both *Rallus* and *Fulica* (but not in *Aramus*) a separate rounded part arises from the dorsal side of the sternocoracoidal process of the sternum and inserts tendinously on the middle of the first vertebral rib. This part apparently acts to draw the rib cage forward.

Summary. The muscle has variations only in its attachments in the three families. However, a distinct muscle, which seems to be associated with *M. sternocoracoideus*, is present in the Rallidae and absent in *Aramus* and *Grus* (*Balearica* is not included).

56. M. coracobrachialis posterior

Medium-sized, irregularly bipinnate muscle with thickly rounded belly and short but strong tendon at dorsal end. Lies partly ventrolateral and partly dorsal to coracoid. Attaches to sternum, to M. supracoracoideus, to coracoid, and to humerus.

Completely deep to M. pectoralis and lies posterodorsal to M. subcoracoideus. Adjacent to and connected with part of dorsal edge of M. supracoracoideus. Superficial to anterior portions of M. sternocoracoideus and to proximal portions of tendon of origin of M. flexor secundariorum.

Origin. Arises fleshily from ventral face of lateral portion of sternal end and dorsolateral face of middle of coracoid. Origin extends posteriorly onto anterolateral corner of plate of sternum.

Insertion. Inserts by strong tendon onto proximal portion of medial bar of humerus.

Action. Assists M. pectoralis in depressing wing, but probably also counters tendency for that muscle to rotate the wing.

Comparisons. In the Gruidae the muscle differs from the condition in Aramus in lacking origin from the sternum and in having the origin extend further dorsad, onto the posterodorsal side of the coracoid. In Balearica (and Aramus) the insertion is on the medial bar of the humerus, but in both species of Grus it inserts slightly more proximally, on the internal tuberosity.

In the Rallidae the muscle differs from that of Aramus in being slightly larger and thicker and in lacking the origin from the sternum. In Fulica more of the origin is in direct contact with the intermediate portion of M. sterno-coracoideus than in Rallus (or Aramus). In both rallids the insertion is on the distal face of the internal tuberosity of the humerus.

Summary. The cranes differ slightly from Aramus and the rallids in the extent of the origin. The rallids have an insertion located slightly distal to that of Aramus, but the cranes are variable for this character. Aramus is unique in having a portion of the origin from the sternum, although a very similar sternal attachment was listed by Fisher (1946) for cathartids.

57. M. latissimus dorsi

Composed of thin, sheet-like dermal part, wide and band-like anterior part, and wider, band-like posterior part. Muscle complex covers most of back. Attaches to sacrum, to dorsal vertebrae, to M. extensor iliotibialis anterior, to skin, and to humerus.

Most of posterior part deep to dermal part and anterior end of posterior part deep to anterior part. Lateral ends of anterior and posterior parts deep to scapular head of M. triceps. Extreme distal end of posterior part deep to M. proscapulohumeralis brevis. Superficial to anterior part of M. rhomboideus profundus, to M. rhomboideus superficialis, to M. dorsalis scapulae, to M. intercostales, to superficial

layer of _M_. _serratus posterior_, to portion of _M_. _spinalis thoracis_, and to portion of _M_. _ilio-costalis_.

Origin. Dermal part arises by thin and extensive aponeurosis, mainly from neural spines of most posterior three thoracic (dorsal) vertebrae but also from anterodorsal edge of _M_. _extensor iliotibialis_ anterior and from aponeurosis of origin and posterior portion of posterolateral edge of belly of posterior part. Posterior part has thin aponeurosis arising from same attachments as previous one, and partially in contact with it. Anterior part arises by mixed fleshy and tendinous fibers from neural spines of last two cervical and first thoracic vertebrae, anterior to origin of previous part but connected to it by thin fascial sheet.

Insertion. Dermal part inserts widely on skin just posterior to axillary regimn. Posterior part has fibers terminating continuously on weak tendon along its posterior edge. Belly gradually becomes smaller, passes under anterior part, and inserts separately by rounded tendon, on small tubercle in usual location (Howard, 1929) in middle of anconal surface of shart of humerus. Anterior part narrows slightly and inserts mostly fleshily on long longitudinal line on anconal side of shaft of upper humerus. Insertions of both posterior and anterior portions partly connect to _M_. _deltoideus major_ and to scapular head of _M_. _triceps_.

Action. Main function is to adduct humerus.

Comparisons. In the Gruidae, _Balearica_ has the dermal part thinner than in _Aramus_, but in _Grus_ it may be a sheet

or a small fasciculus of the posterior part, or it may be absent. In the three cranes the origins of the anterior and the posterior parts are adjacent (widely separated in *Aramus*). The insertion of the anterior part is the same in the cranes and *Aramus*. The posterior part in both *Balearica* and *G. americana* inserts mainly on the underside of the anterior part, and the tendinous insertion on the humerus is joined to it. In *G. canadensis* (and *Aramus*) the posterior part inserts proximal to the anterior part, with little or no attachment to it.

In the Rallidae all parts of this muscle are better developed in *Fulica*, and the origins of the anterior and posterior parts are closer together than in *Rallus* or *Aramus*. In both rallids the dermal part resembles that part in *Aramus*, except that in neither is any of the posterior edge of the posterior part deep to it. In *Fulica* (and *Aramus*), but not in *Rallus*) the dermal part extends posteriorly to the sacrum. In *Rallus* the posterior part may or may not attach strongly to the anterior part, but it always continues proximad to insert independently. In *Fulica* the posterior part may attach weakly or not at all to the anterior part, and its insertion may be continuous with that part or independent (in *Aramus* the insertion is independent with very little connection to the anterior part). In both rallids the insertion of both parts is located further distally than in *Aramus*, near the base of the deltoid crest.

Summary. The development of the dermal part, the extent of the origins, and the interconnections of the insertions of

the anterior and posterior parts are all variable, even within the Gruidae and Rallidae. The Rallidae differ distinctly from the other two families in having the insertions of the anterior and posterior parts near the base of the deltoid crest, instead of on the middle of the shaft as in Aramidae and Gruidae.

58. *M. cucullaris*, axillary part

Flattened muscle with irregular shape. Lies on dorsal surface of shoulder region. Attaches to vertebrae in shoulder region, to *M. tensor patagii brevis*, to *M. deltoideus major*, to scapula, and to furculum.

Right and left muscles contact across mid-line. Anterior edge deep to posterior edge of *M. dermo-temporalis*. Adjoins anterior edge of *M. rhomboideus superficialis*, and partly connects anterolaterally to *M. pectoralis*, *M. tensor patagii brevis*, and *M. deltoideus major*. Superficial to anterior edge of *M. rhomboideus profundus*, to posterior end of *M. spinalis cervicis* and anterior end of *M. spinalis thoracis*, and to some of *Mm. ascendentes*.

Origin. Arises by thin aponeurosis from dorsolateral edges of neural spines of thirteenth through fifteenth cervicals and from connective tissue between the spines.

Insertion. Inserts mostly fleshily onto dorsal edge of anterior extent of scapula, sends small fascial sheet over dorsal end of furculum, and inserts fleshily onto anteromedial edge of dorsal half of furculum. Ventral surface connects closely to wall of clavicular air sac.

Action. May constrict clavicular air sac by drawing together scapulae and free ends of furculum.

Comparisons. In the Gruidae the muscle in G. americana only, has a reduced anterior portion. In Grus the location of the origin seems to be further anterior than in Balearica (or Aramus). In Balearica the muscle has a unique connection to a fascial sheet extending from the shoulder region to the skin. In Balearica only, the posterior edge of the belly lacks a definite separation from M. rhomboideus superficialis. The anteroventral portion in Balearica differs from that in Aramus in being closely connected to the posterior end of M. dermo-temporalis; the latter muscle is not present in this region in Grus. The extent of the insertion is quite similar in both cranes and in the limpkin.

In the Rallidae the muscle in Fulica is thicker but is much less extensive than in Rallus (or Aramus). Uniquely in Rallus a large portion of M. serratus profundus extends under the muscle. In both rallids the insertion is more restricted than in Aramus, occupying only the dorsal fifth of the furculum.

Summary. The muscle is specialized to a small degree in both Grus americana and Fulica. The most distinctive variation is the small furcular attachment in the Rallidae, compared to the considerably larger one in Aramus and the Gruidae.

59. *M. rhomboideus superficialis*

Wide but short and thin sheet of muscle. Located between scapula and spinal column. Attaches to thoracic vertebrae and to scapula.

Partly deep to portions of anterior and posterior parts of *M. latissimus dorsi*. Adjoins posterior edge of axillary part of *M. cucullaris* and dorsal edge of *M. dorsalis scapulae*. Superficial to all but anterior and posterior portions of *M. rhomboideus profundus*.

Origin. Arises by thin aponeurosis from connective tissue associated with neural spines of sixteenth through nineteenth vertebrae. Tendon of origin partly connected to origin of *M. rhomboideus profundus*.

Insertion. Mainly by fleshy attachment to dorsomedial edge of all but posterior 10 mm of blade of scapula.

Action. Draws blade of scapula dorsomediad and braces it.

Comparisons. In the Gruidae the insertion in *G. americana* is distinct in extending to the distal tip of the bone.

In the Rallidae the muscle is essentially the same as in *Aramus*. Uniquely in *Rallus* the insertion ends just anterior to an abrupt bend in the scapula.

Summary. The muscle is similar in all three families, but in *G. americana* the insertion is specialized, being much longer than in the other species used in this study.

60. *M. rhomboideus profundus*

Wide but short and thin sheet of muscle. Located between scapula and spinal column. Attaches to thoracic vertebrae and to scapula.

Small portion of anterior end deep to cervical part of *M. cucullaris*. Deep to *M. rhomboideus superficialis* except for small anterior and posterior regions, and posterior portion deep to posterior part of *M. latissimus dorsi*. Superficial to posterior end of *M. spinalis cervicis* and anterior end of *M. spinalis thoracis*, to some of *Mm. ascendentes*, and to posterior region of *M. serratus profundus*.

Origin. Arises by thin and very short aponeurosis from connective tissue associated with fifteenth through twentieth vertebrae. This tendon connects to origin of *M. rhomboideus superficialis*.

Insertion. Anterior portion of insertion tendinous, on dorsomedial edge of scapula between insertions of *M. rhomboideus superficialis* and *M. serratus profundus*. Insertion continues posteriad along edge of scapula, becomes fleshier, and moves onto all of medial face of scapula in posterior fourth of blade. Posteroventral portion of insertion contacts scapular attachment of posterior part of *M. serratus posterior*.

Action. Draws blade of scapula dorsomediad and slightly anteriad.

Comparisons. In the Gruidae the origin in *Balearica* (and *Aramus*) ends posteriorly near the level of the tip of

the scapula, but in _Grus_ it is more extensive, ending on the vertebra next to the sacrum.

In the Rallidae the insertion is entirely fleshy and intimately connected anteriorly to _M. serratus profundus_ (anterior portion is tendinous in _Aramus_ and has weaker connection to the latter muscle).

Summary. The most distinct variation among the three families is the somewhat larger origin in _Grus_. All the genera examined agree in what Berger (1956a) pointed out as an unusual feature: _M. rhomboideus profundus_ is larger than _M. rhomboideus superficialis_.

61. _M. coracobrachialis anterior_

Somewhat small but wide and thick muscle, slightly wider at posterior end. Located on dorsolateral corner of shoulder joint. Attaches to coracoid, to capsule of shoulder joint, and to _M. biceps_.

Ventral two-thirds of muscle deep to _M. biceps_, and dorsal one-third deep to _M. pectoralis_. Posterior end ventral to posterior end of _M. deltoideus minor_.

Origin. Arises by strong tendon from side of dorsal end of coracoid and by connective tissue from capsule of shoulder joint. Side of proximal end of muscle fused to inner side of tendon of origin of _M. biceps_.

Insertion. Attaches to very large area on palmar face of humerus, between bicipital crest and anterior half of deltoid crest. Most of attachment fleshy, but more tendinous around edges.

Action. Draws humerus anteriad.

Comparisons. In the Gruidae the origin is entirely fleshy from the coracoid instead of tendinous as in *Aramus*. In *Balearica* (and *Aramus*) the origin is from the side of the dorsal end of the coracoid, but in *Grus* the origin is from the dorsal face of the dorsal end.

In the Rallidae the muscle in *Rallus* is very similar to that of *Aramus*, but *Fulica* differs in having the origin somewhat wider and in having the entire dorsal edge of the muscle in contact with *M. coracobrachialis anterior*.

Summary. The muscle is closely comparable in all genera included in this study.

62. *M. deltoideus minor*

Small and flattened, elongately triangular muscle. Lies over dorsolateral side of shoulder joint. Connects to coracoid, to furculum, to coracoclavicular ligament, and to scapula.

Completely deep to belly of *M. tensor patagii brevis*, and anteromedial region deep to and connected to *M. deltoideus major*. Posterior end contacts dorsal edges of *M. pectoralis* and *M. coracobrachialis anterior*. Superficial to and strongly connected to insertion of anterior part of *M. supracoracoideus*.

Origin. Arises fleshily and tendinously from dorsal face of furculum posterior to origin of *M. tensor patagii brevis*, from dorsomedial corner of dorsal end of coracoid, from coracoclavicular ligament, from small area on

anterolateral aspect of acromion of scapula, and from small area on medial side of procoracoid process of coracoid.

Insertion. Mixed fleshy and tendinous, on proximal edge and small portions of both faces of deltoid crest of humerus. Connected to insertions of anterior part of M. supracoracoideus and M. pectoralis.

Action. Draws humerus anteriad and rotates anterior edge upward.

Comparisons. In the Gruidae the origin in Balearica (and Aramus) differs from that of Grus in arising partly from the dorsal face of the furculum. In G. americana only, there is some origin from the side of the furculum. In Balearica and G. americana there is no origin from the procoracoid process of the coracoid, but in G. canadensis (and Aramus) a small portion arises from that process. The portion from the procoracoid arises by a separate head in G. canadensis only. The portions of the origins from the dorsal end of the coracoid and from the scapula are represented in all three cranes (and Aramus). In Grus (and Aramus), but not in Balearica, the insertion extends to the edges of the anconal face of the deltoid crest.

In the Rallidae the belly in Fulica is wider than in Rallus (or Aramus) and is connected for its entire length to the tendon of M. supracoracoideus and to the length of M. coracobrachialis anterior. In Rallus the origin differs from that of Fulica (and Aramus) in lacking the attachment to the procoracoid. In both rallids the insertion is

smaller and more restricted than in *Aramus*, attaching only to the proximal edge of the deltoid crest.

Summary. There are variations in the points of origin within the cranes, even within *Grus*. The insertion is elongate in Gruidae and Aramidae but is short in Rallidae. *Fulica* is somewhat specialized in having the muscle wider than in the other genera. All these variations are relatively minor.

63. *M. subscapularis* and
M. proscapulohumeralis

A small triangular muscle with distal portion separated into two heads. Located in angle between scapula and humerus and on underside of scapula. Attaches to scapula, to humerus, to small tendon from scapular head of *M. triceps*, and to *M. serratus anterior*.

Berger (1956a) pointed out that *M. proscapulohumeralis* of Fisher and Goodman (1955) is actually the external head of *M. subscapularis* (Gadow, 1893), and that the muscle they listed as *M. subscapularis* is the internal head.

External head (*M. proscapulohumeralis*) superficial to all, or all but posterior edge, of portion of internal head not covered by scapula. Partly deep to *M. dorsalis scapulae* and to scapular head of *M. triceps*. Superficial to some of anterior *Mm. intercostales*.

Origin. External head arises fleshily from ventrolateral edge of neck and anterior portion of blade of scapula. Internal head arises from whole width of medial side of neck and anterior third of scapular blade.

Insertion. Two heads fuse, then belly narrows abruptly into strong tendon that inserts on proximal end of internal tuberosity of humerus.

Comparisons. In the Gruidae Balearica and G. canadensis (and Aramus) have the origin of the external head arising from the neck and from a small anterior portion of the blade of the scapula. In G. americana this origin apparently extends farther posterior, since Fisher and Goodman (1955) stated that it arises partly from the "second and third fifths of the length of the scapular blade." The origin of the internal head seems to be similar in the three cranes and Aramus. In Balearica the insertion is in the bottom of the capital groove, and in Grus it is on the posterior border of the groove (on the internal tuberosity in Aramus).

In the Rallidae the external head in Rallus (and Aramus) arises partly from the lateral face of the scapula, but in Fulica the origin is restricted to the ventral edge. The origin of the internal head and the single insertion are quite similar in both rallids (and Aramus).

Summary. Grus americana is specialized in having the origin of the external head located posterior to that in the other two cranes and in the non-gruids. Fulica has some different specialization of the external origin. Aramus agrees with the rallids in having the insertion on the internal tuberosity instead of in the capital groove as in the cranes, but this difference is very slight.

64. _M. proscapulohumeralis (brevis)_

Very small, narrow band of muscle of variable size among different specimens. Lies in angle between scapula and humerus. Attaches to scapula, to humerus, and to _M. triceps_.

Berger (1956a) pointed out that the name _M. proscapulohumeralis_, if not used according to Fisher and Goodman (1955) for the external head of _M. subscapularis_, is available for the muscle referred to as _M. proscapulohumeralis brevis_ by those authors.

Mitchell (1901; _M. scapuli-humerales anterior_) found the muscle to be large in his dissections of _Aramus_ but reported that Fürbringer found it to be small. The size of the muscle is somewhat varied in the specimens dissected in this study.

Lies completely deep to scapular head of _M. triceps_.

Origin. Arises fleshily and tendinously from small line on ventral edge of neck of scapula, just ventral to scapular origin of _M. triceps_ and tendinously connected to belly of that muscle.

Insertion. By fleshy and tendinous attachment onto small area on anconal face of shaft of humerus, between pneumatic fossa and insertion of posterior part of _M. deltoideus major_. This attachment is in the usual location of the medial crest, which is flattened in _Aramus_.

Action. Adducts humerus.

Comparisons. In the Gruidae the muscle in Balearica and both species of Grus (Berger, 1956b) apparently is not always present (always present, but variable in size in Aramus). In Balearica the only origin is from a small area in the center of the lateral face of the neck of the scapula, and in G. americana a portion of the origin is from the dorsolateral portion of the scapular neck. In G. canadensis (and Aramus) the only origin is from the ventral edge of the anterior region of the neck, and this attachment forms a portion of the origin in G. americana. In all three cranes (and Aramus) the insertion is similarly located, but in only G. americana is it tendinous.

In the Rallidae the muscle is much wider than in Aramus, but the origin is from the same area of the scapula. In Fulica there is more extensive connection to the belly of the scapular head of M. triceps than in Rallus (or Aramus). In both rallids the muscle has an elongate, fleshy attachment to the medial ridge, internal to the insertion of M. latissimus dorsi and intimately adjoined to the anterior end of the humeral origin of M. triceps (the insertion in Aramus is compact and external to the insertion of M. latissimus dorsi). The insertion in Fulica is slightly more proximal than in Rallus.

Summary. The muscle is similarly small in Aramus and the cranes, but it is much larger in the Rallidae, in which family Mitchell (1901) stated that the muscle reaches maximum development in the Gruiformes. Aramus also agrees with

the gruids in having a small insertion than in Rallidae and in having it located external to the insertion of *M. latissimus dorsi* instead of internal to it as in Rallidae. The origin is variable within the Gruidae, and even within *Grus*.

65. *M. dorsalis scapulae*

Medium sized, flattened and triangular muscle; somewhat pinnate in posterior half of belly. Lies posteroventral to angle of humerus and scapula, and connects the two bones. Attaches to scapula, to humerus, and to *M. expansor secondariorum*.

Posterior half deep to main parts of *M. latissimus dorsi*. Anterior end deep to scapular head of *M. triceps*. Superficial to posterior end of *M. subscapularis* and to portions of *M. serratus anterior* and *posterior* and *Mm. intercostales*. Muscle is penetrated near ventral edge of middle of belly by tendon of *M. expansor secundariorum.*

Origin. Arises fleshily from entire area of lateral face of blade of scapula and by deep tendinous sheet arising from posterior aspect of ventral edge of blade. Most of dorsal edge of origin contacts ventral edge of insertion of *M. rhomboideus superficialis*. Ventral edge of origin contacts insertion of *M. serratus posterior*.

Insertion. Bundles in posterior half of belly converge to strong tendon that proceeds to insert in center of anconal side of bicipital crest, in common with fleshy insertion of bundles from anterior half of muscle.

Action. Adducts and rotates humerus, raising posterior edge of wing.

Comparisons. In the Gruidae the pinnate condition of the posterior half of the belly, in Balearica (and Aramus), is not mentioned for Grus. In Balearica and G. canadensis the tendon of M. expansor secundariorum penetrates the edge of the posterior part in the distal half of the belly (in the middle of the belly in Aramus). This character was not mentioned for G. americana, but is presumably present. In Balearica (and Aramus) the muscle originates from the entire lateral face of the scapular blade, but in Grus it originates from all but the dorsal half of the posterior portion. In Balearica (and Aramus) there is a deep tendinous portion of the origin, but this is not mentioned for either species of Grus. In all three cranes the insertion is similar to, but slightly more proximal than, the attachment in Aramus.

In the Rallidae the belly is somewhat pinnate (as in Aramus), and the tendon of M. expansor secundariorum penetrates the edge of the middle of the distal half of the belly (penetrates edge of middle of belly in Aramus). In Fulica (and Aramus) the deepest portion of the origin is by a strong tendinous sheet, but this tendon is quite weak in Rallus. In Rallus the insertion is near the same level as in Aramus, but it is on the shaft of the humerus, just off the bicipital crest. In Fulica the insertion is more proximal, on the outer edge of the most proximal portion of the anconal face of the bicipital crest.

Summary. The basic pattern of this muscle is similar in all genera studied, and the few minor variations present are inconsistent within the families.

66. _M_. _serratus_ _posterior_

Composed of widely band-like superficial part and wider and thicker deep part; superficial part has small, fleshy or fascial dermal component. Covers center of outer body wall. Attaches to ribs, to fascia over intercostal muscles, to scapula, to skin, and loosely to _M_. _serratus_ _anterior_.

Superficial part covers most of deep part. Dorsal portions deep to posterodorsal portion of _M_. _dorsalis_ _scapulae_ and to posterior and dermal parts of _M_. _latissimus_ _dorsi_. Ventral edge adjoins dorsal edge of _M_. _obliquus_ _abdominis_ _externus_, and anterior edge runs between heads of _M_. _subscapularis_ to join _M_. _serratus_ _anterior_. Superficial to some of _Mm_. _intercostales_ _externi_.

Origin. Superficial part arises fleshily from uncinate process and middle of lateral face of second true rib and by aponeurosis from similar place on third true rib. Also arises by fascia between those ribs. Deep part arises by thin aponeurosis that attaches by connective tissue to ventrolateral faces of last free rib, to first three true ribs, and to uncinate process of second true rib. Ventral edge of aponeurosis arises from superficial side of _M_. _obliquus_ _abdominis_ _externus_.

Insertion. Superficial part inserts by very thin and narrow (3 mm) aponeurosis that arises from anterodorsal corner of belly and attaches to deep part and to ventral edge of posterior end of scapula. Dermal component, equivalent to anterodorsal corner of belly, attaches to skin by fascia

associated with dermal part of _M_. _latissimus dorsi_. Deep part inserts on ventral edge of scapula. Posterior portion of attachment fleshy, and more anterior portion attaches by thin aponeurosis that is continuous with _M_. _serratus anterior_ as it passes through _M. subscapularis_.

Action. Braces scapula and draws blade ventrad, and may also expand rib cage (Fisher, 1946). Dermal component adjusts scapular feathers.

Comparisons. In the Gruidae the muscle in _Balearica_ and _G_. _americana_ (and _Aramus_) is separated into a superficial part with a dermal component and a deep part, but in _G_. _canadensis_ there is one main part, and the dermal component is larger and somewhat separate. The origin of the superficial part is variable, arising in _Balearica_ from the third through the sixth true ribs, and in _G_. _americana_ from the fourth through seventh (?true) ribs (from the second and third true ribs in _Aramus_). In _G_. _canadensis_ the whole muscle arises in a manner similar to that of the superficial part in _G_. _americana_. The deep part arises in _Balearica_ from the first through sixth true ribs, and in _G_. _americana_ it arises from the fourth through sixth (?true) ribs (in _Aramus_ it arises from the last free rib and the first three true ribs). The insertion of the superficial part in _Balearica_, but not in _Grus_ (or _Aramus_), is mainly on the posterodorsal edge of _M_. _dorsalis scapulae_, but like the single muscle in _G_. _canadensis_ (and the superficial part in _Aramus_), there is insertion on the ventral edge of the posterior extent of the scapula. In _G_. _americana_

only, this part passes superficial to a portion of *M. dorsalis scapulae* and inserts on the posterodorsal face of the scapula. The deep part in *Balearica* (and *Aramus*) inserts on nearly the full length of the scapula, but this attachment is restricted to the posterior half of the blade in *G. americana*.

In the Rallidae the muscle is divided into a main part and a separate dermal part (in *Aramus* it is divided into two main parts, one of which has a dermal component). In *Rallus* the main part is wide and arises from the first through fifth true ribs, but in *Fulica* it is narrow and more posterior, arising from the third through sixth true ribs (this origin seems equivalent to the origin of the deep part in *Aramus*). In both rallids the dermal part is a superficial band, smaller than the main part, arising mainly from superficial fascia of *M. obliquus abdominis* externus at the posteroventral corner of the main part. In *Rallus* the dermal part inserts entirely on the skin, but in *Fulica* it has an additional small aponeurotic connection to the ventral edge of the scapula (the latter resembles the double insertion of the superficial part in *Aramus*).

Summary. There is variation in the manner of division of the muscle. However, the separate dermal part found in *Grus canadensis* and the two rallids is probably equivalent to the superficial part of *Aramus* and the other two cranes. Apparently the portion of the superficial part inserting on the scapula may instead be fused to the deep part. The dermal part in *Fulica* seems to be intermediate, since it has

a very small scapular insertion. The total area of origin is at least somewhat unequal in every species included here, but the total area of insertion is rather similar in all. In _Grus americana_ only, the insertion is more posterior and partly on the dorsal portion of the scapular blade.

67. _M. serratus profundus_

Composed of four short, flat fasciculi of approximately equal size; parts are separate but somewhat overlapping. Located between scapula and body wall. Attaches to some of _Mm. ascendentes cervices_, to some of _Mm. levatores costarum_, to ribs, to vertebrae, and to scapula.

Partly deep to _M. rhomboideus profundus_, _M. subscapularis_, _M. dorsalis scapulae_, and cervical part of _M. cucullaris_. Superficial to some of _Mm. intercostales externi_, to some of _Mm. levatores costarum_, and to anterior region of _M. ilio-costalis_.

Origin. First fasciculus arises tendinously from transverse process of sixteenth cervical and has mixed origin from free rib of seventeenth. Second fasciculus originates tendinously from free ribs of seventeenth and eighteenth vertebrae and from adjacent portions of _M. ascendentes cervices_. Third fasciculus arises by fleshy and tendinous fibers from first true rib. Fourth fasciculus arises tendinously from fascia connecting first two true ribs and also by mixed origin from second true rib and intercostal fascia posterior to it.

Insertion. All four fasciculi insert fleshily on large area in middle of medial face of scapula, between origin of M. subscapularis and insertion of M. rhomboideus profundus.

Action. Adducts scapula, draws it forward, and probably braces it.

Comparisons. In the Gruidae (and Aramus) the muscle is divided into four parts, but in Balearica the first three are indefinitely separable. In the three cranes the fourth part is very small. The first three parts are of about the same size in Balearica, but in Grus the first part is largest (all four parts are about the same in Aramus). In Balearica and G. americana the origin of the complex involves the first two true ribs, but in G. canadensis it involves the first three (in Aramus the origin is from the last two free ribs and the first two true ribs). The insertion is similar in the three cranes (and Aramus).

In the Rallidae the muscle is divided into four fasciculi, but they are larger than in Aramus. In Rallus the first part is largest, but all are about the same size in Fulica (and Aramus). In Rallus (and Aramus) all fasciculi are compact and separate, but in Fulica the second and third are composed of loosely connected bundles, and the last two are connected to each other. In both rallids the length of the insertion is greater than in Aramus, but the attachment is only on the dorsomedial edge of the scapula (on the full width of the medial face in Aramus).

Summary. The division of the muscle into four fasciculi is evident in all the genera studied, with only minor variations

in the arrangement of the parts. The rallids are distinct from *Aramus* and the cranes in having the insertion occupying only the edge of the scapula.

68. *M. serratus anterior*

Single fleshy fasciculus, narrowly band-like in dorsal half. Lies on dorsolateral side of anterior ribs. Connects to ribs, to scapula, and to *M. serratus posterior*.

Deep to *M. dorsalis scapulae*, and dorsal end deep to external head of *M. subscapularis*. Adjoins posterior edge of *M. scalenus* and continuous with *M. serratus posterior*. Superficial to some of *Mm. intercostales externi*.

Origin. Arises by mixed fleshy and tendinous fibers from ventral portions of last free rib and first true rib, in contact with posterior edge of *M. scalenus*.

Insertion. Band-like belly becomes tendinous near dorsal end, passes between external and internal heads of *M. subscapularis*, and attaches to small section of ventral edge of anterior extent of scapular blade.

Action. May pull scapula posteroventrad or expand rib cage.

Comparisons. In the Gruidae the origin in *Balearica* (and *Aramus*) comes from the first two true ribs, but in *G. americana* the muscle arises from the second, third, and sometimes the fourth (?true) ribs, and in *G. canadensis* it originates from the first three true ribs. The muscle is rather compact in *Balearica* and *G. americana* (and *Aramus*), but in *G. canadensis* it arises by three slips. In *Balearica* (and

Aramus) this muscle is continuous with M. serratus posterior by a thin but distinct fascial sheet; this feature is not mentioned for either species of Grus. In G. canadensis the insertion is apparently located further anterior than in the other two cranes (or Aramus).

In the Rallidae the arrangement of this muscle differs from that of Aramus only in being larger and fleshy to the point of insertion (upper end is aponeurotic in Aramus).

Summary. The Rallidae differ from the Gruidae and Aramidae in having the muscle larger and fleshier. Otherwise there is good agreement among the genera used in this study.

69. M. subcoracoideus

Very short but thick muscle of somewhat pyramidal shape. Located posteroventral and somewhat medial to shoulder joint. Attaches to coracoid, to sterno-coraco-clavicular membrane (Woolfenden, 1961) and to humerus.

Partially deep to M. coracobrachialis posterior. Superficial to some of coracoidal portion of tendon of M. expansor secundariorum.

Origin. Arises fleshily from elongately oval area on posteromedial face of shaft of coracoid and procoracoid process. To varying degree, depending on extent of ossification of procoracoid, muscle also arises from thickened posteromedial edge of sterno-coraco-clavicular membrane.

Insertion. Thick belly narrows abruptly into small, rounded tendon that attaches strongly to proximal face of internal tuberosity of humerus. Attaches on well marked

scar, lying on inner side of scar for _M_. _subscapularis_.

Action. Raises anterior edge of wing by rotating humerus, and may also aid in downstroke of wing.

Comparisons. In the Gruidae the muscle in _Balearica_ (and _Aramus_) arises from a large area of the posteromedial surface of the shaft of the coracoid and procoracoid process and from the sterno-coraco-clavicular membrane. In both species of _Grus_ the muscle is smaller, arising no further ventral than the procoracoid, and there is no origin from that process. In _Balearica_ alone, the origin extends onto the edge of the ventromedial corner of the proximal end of the scapula. The insertion is similar in all three cranes (and _Aramus_), but Berger (1956b) stated that in _G_. _canadensis_ the tendon may sometimes fuse with that of _M_. _subscapularis_.

In the Rallidae the muscle arises mainly from the sterno-coraco-clavicular membrane and attaches loosely to the ventral region of the posterior face of the shaft of the coracoid (arises in _Aramus_ mainly from the coracoid and procoracoid process, with only a small attachment to the membrane). In the two rallids a portion of the origin (not present in _Aramus_) arises strongly from a small (subcoracoidal) process. This origin is better developed in _Rallus_, extending from the medial edge of the coracoid just below the level of the sterno-coracoidal impression. In _Rallus_ the insertion is on the internal edge of the proximal face of the internal tuberosity, and in _Fulica_ it is on the internal face (the insertion is on the proximal face of the process in _Aramus_).

Summary. The area of origin of this muscle is quite variable. It arises in *Aramus* and *Balearica* from a large area of the coracoid, but in *Grus* the origin is smaller and more dorsal, and in the Rallidae it is smaller and more ventral. The rallids differ from *Aramus* and the cranes in having the origin mainly from the sterno-coraco-clavicular membrane and in having it arise partly from a subcoracoidal process. The insertion in the rallids also differs from that of *Aramus* and the cranes in not being strictly on the proximal face of the internal tuberosity of the humerus.

70. *M. biceps*

Large and elongate muscle with spindle-shaped belly enclosed by thick, superficial fascia; proximal end composed of thick tendinous band, and distal end becomes two small, rounded tendons. Lies along anteroventral portion of upper arm. Attaches to coracoid, to humerus, to *M. coracobrachialis anterior*, to *M. pectoralis*, to *M. tensor patagii longus*, to radius, and to ulna.

Proximal end deep to inserting end of *M. pectoralis*. Belly lies anterior to external head of *M. triceps* and adjoins anterodistal edge of *M. deltoideus major*. Distal ends of inserting tendons pass between *M. extensor metacarpi radialis* and *M. brachialis*. Proximal tendon partly superficial to *M. coracobrachialis anterior*.

Origin. Arises by strong tendon from narrow line of bicipital area on dorsal end of coracoid, in common with anterior edge of origin of *M. coracobrachialis anterior*.

Another head arises by small tendon from edge of bicipital crest near its junction with internal tuberosity, and this tendon gives rise to fleshy belly but is also connected by strong tendinous sheet to tendon from coracoid. Just distal to head of humerus two heads fuse to form single belly, which receives portion of insertion of _M. pectoralis_. Slightly distal to this point, biceps slip leaves belly and attaches to _M. tensor patagii longus_.

Insertion. In distal half belly gradually tapers down to two small but very strong, rounded tendons that pass between _M. extensor metacarpi radialis_ and _M. brachialis_. One tendon inserts on bicipital tubercle on inner side of proximal end of radius. Second tendon, which may be ossified, inserts mainly on usual bicipital facet on proximal end of palmar side of ulna, but has small branch that inserts on radius, alongside previous tendon.

Action. Flexes forearm.

Comparisons. In the Gruidae the belly is larger in _Balearica_ (and _Aramus_), and the two heads of origin are apparently more closely connected than in _Grus_. In _G. americana_ the anterior origin may be sometimes strongly fused to either _M. pectoralis_ or _M. tensor patagii longus_, but these conditions were not mentioned for _G. canadensis_ and were not found in the other genera in this study. In _Balearica_ the fleshy belly extends distad, enclosing the tendon to the point of its penetration of the forearm musculature, but in _Grus_ (and _Aramus_) the belly ends well before this point.

Some ossification is at least sometimes present in the proximal portion of at least one of the tendons in *Balearica* and *G. canadensis* (and *Aramus*), and probably in *G. americana* as well. In *Balearica* the tendon inserting on the radius divides into two branches, and the one to the ulna gives off a small branch to the radius (in *Aramus* the radial tendon is simple, but the one to the ulna divides as in *Balearica*). Both the tendons are apparently simple in *Grus*.

In the Rallidae the tendon from the coracoidal origin is connected to *M. coracobrachialis anterior* only at the anterior end (connected to the whole length of the belly in *Aramus*), and the two heads of origin are continuous by means of a connective tissue sheet (in *Aramus* the two origins are largely separate). In both *Rallus* and *Fulica* the belly extends into the forearm musculative (belly ends well before this point in *Aramus*). In *Rallus* the two main tendons of insertion are connected (essentially separate in *Aramus*), and in *Fulica* they are even more strongly attached to each other. In *Rallus* the ulnar tendon is simple, but the radial tendon widens at its insertion and gives off a small branch to the ulna (only the ulnar tendon is divided in *Aramus*, giving off a branch to the radius). In *Fulica* the two main tendons remain closely adherent all the way to the insertion. Neither rallid has ossification of these tendons (at least one is ossified in *Aramus*).

Summary. Minor details of the belly and attachments of this muscle are subject to interfamilial and to intrafamilial

variation, and at least in *Grus*, to individual variation as well. The Rallidae differ from *Aramus* and the cranes in having very little fusion to *M. coracobrachialis anterior*, in having the two origins continuous with each other, and in lacking ossification of the inserting tendons. The length of the belly is strikingly longer in *Balearica* and the two rallids than in *Aramus* and *Grus*.

71. *M. deltoideus major*

Muscle composed of large, thick anterior part, triangular in dorsal view, and much smaller, flattened posterior part. Located on dorsal side of shoulder and proximal half of upper arm. Attaches to scapula, to furculum, and to humerus.

Posterior part appears to represent posteromedial section of belly of anterior part, and two parts contact each other closely. Anterolateral portion of muscle deep to belly of *M. tensor patagii brevis*. Proximal end of belly contacts cervical part of *M. cucullaris*. Anteroproximal edge contacts belly of *M. deltoideus minor* and insertion of *M. supracoracoideus*. Anterodistal edge parallels belly of scapular head of *M. triceps*. Proximal end of anterior part lies superficial to proximal end of *M. deltoideus minor* and proximal end of posterior part lies superficial to origin of scapular head of *M. triceps*.

Origin. Anterior part arises, in contact with origins of *M. tensor patagii brevis* and cervical part of *M. cucullaris*, by fleshy and tendinous fibers from dorsal face and medial side of dorsal extent of furculum and from

anterolateral face of acromion of scapula. Deepest portion of origin arises by small band of strong tendon from anterior tip of acromion. Another small but strong band of tendon arises from dorsolateral edge of scapula about 2 cm from anterior end and enters posterior edge of anterior part, near proximal end. Posterior part, although small, arises mostly fleshily from much larger area of lateral face of proximal end of head and portion of neck of scapula. This origin contacts insertion of M. rhomboideus superficialis and origin of scapular head of M. triceps.

Insertion. Anterior part inserts indirectly by tendinous attachments to capsule of humeroscapular joint and directly by fleshy attachment to large area of anconal face of humerus, extending from level of middle of pneumatic foramen to just beyond middle of length of shaft, and from edge of deltoid crest to line of attachment of M. latissimus dorsi. Anteroventral edge of distal half of belly attaches to aponeurosis connecting to scapular head of M. triceps. Posterior part inserts on small portion of area described above, just external and somewhat anterior to anterior fourth of insertion of M. latissimus dorsi.

Action. Adducts humerus, pulls it somewhat dorsad, and rotates it to raise anterior edge of wing.

Comparisons. In the Gruidae the muscle in Balearica (and Aramus) is divided into two parts, but in Grus the two are apparently fused. The posterior part in Balearica is much thinner than that of Aramus. In G. americana only,

there is a dermal component. In _Balearica_ the furcular origin is restricted to the posterior edge, but it arises at least partly from the dorsal end in _Grus_ (and _Aramus_). In _Balearica_ only, the muscle arises partly from the capsule of the shoulder joint. The deep tendon of origin from the acromion in _Aramus_ is not found in the cranes. The insertion in the three cranes is similar to that of _Aramus_, but in _Balearica_ the attachment of the posterior part is anterior to and narrower than the same insertion in _Aramus_.

In the Rallidae the muscle differs from _Aramus_ in being undivided. In the rallids the muscle is longer than in _Aramus_, extending for two-thirds the length of the humerus in _Rallus_ and only slightly less than that in _Fulica_. The proximal end of the insertion in both rallids passes over a narrow but strong tendon of the scapular head of _M_. _triceps_ (this tendon is lacking in _Aramus_). In both _Rallus_ and _Fulica_ the distal two-fifths of the belly has very little fleshy attachment and inserts mainly by the aponeurosis to the scapular head of _M_. _triceps_.

Summary. The muscle in _Balearica_ has some unique differences in its origin, and _Grus americana_ has a dermal component that is lacking in the others. The two rallids differ slightly from _Aramus_ and the cranes in having the posterior portion of the insertion mainly aponeurotic instead of fleshy. There is no _os humeroscapulare_ associated with the origin in any of the genera included in this study.

72. _M_. _triceps_

Complex muscle composed of three heads, large and elongate scapular head, similar but bipinnate external head, and very small internal head. Scapular head lies along posterodorsal edge, external head along posteroventral edge, of upper arm. Internal head lies against anconal face of distal end of humerus. The complex attaches to scapula, to humerus, to _M_. _anconaeus_ _coracoideus_, to joint capsule of elbow, and to ulna.

In dorsal view anterior edge of proximal half of scapular head lies ventral to _M_. _deltoideus_ _major_, and internal head partly deep to scapular head. _M_. _latissimus_ _dorsi_ inserts between two. Distal ends of all three heads partly deep to belly of _M_. _expansor_ _secundariorum_. Anterior end of scapular head superficial to portion of _M_. _subscapularis_ and to all of _M_. _proscapulohumeralis_. Posterior ends of scapular and internal heads both superficial to external head. In ventral view internal head posterior and partly deep to proximal portion of _M_. _biceps_.

Origin. Scapular head originates dorsal to origin of _M_. _proscapulohumeralis_ by mixed fleshy and tendinous fibers from small area of ventrolateral edge of scapula, at junction of head and neck. Two tendons also contribute to origin; one is small band from scapula and connective tissue over _M_. _subscapularis_, and other is wider sheet (7 mm) arising obliquely from insertion of posterior part of _M_. _latissimus_ _dorsi_ and from humerus for 10 mm distad. Internal head originates

mostly fleshily from large area on internal side of palmar face of humeral shaft, from palmar side of distal half of bicipital crest, and from distal portion of pneumatic fossa. External head arises fleshily, from distal continuation of origin of previous part, from small area of distal shaft, and olecranal fossa.

Insertion. Ossified tendon arises within distal two-thirds of belly of scapular head but finally leaves distal end of belly as flattened tendon, stiff but unossified, that passes through external tricipital groove. Tendon attaches to joint capsule of elbow and inserts strongly on tricipital facet at dorsal side of proximal end of ulna. Another ossified tendon arises on superficial aspect of internal head, passes through internal tricipital groove as unossified band, attaches to joint capsule of elbow, and inserts strongly onto distal tip of olecranon of ulna. External head sends fleshy fibers to tendons of both scapular and internal heads, as well as to thinner tendinous sheet that connects those two tendons and attaches to ulna between their attachments. Minute tendon of *M. anconaeus coracoideus* inserts on this sheet.

Action. Extends forearm.

Comparisons. In the Gruidae the internal head in *Balearica* (and *Aramus*) is almost entirely free from the belly of the external head, but in *G. americana* the two bellies are somewhat fused distally, and in *G. canadensis* they are completely fused. In *Balearica* (and *Aramus*) the internal tendon

of the scapular head and the superficial tendon of the internal head are both partly ossified, but in _G. canadensis_ ossification is mentioned only for the tendon of the internal head, and none is mentioned for _G. americana_. The attachment to the common tendon by _M. anconaeus coracoideus_ is probably present in all, but is unknown for _G. americana_.

In the Rallidae the scapular and internal heads are considerably larger than in _Aramus_, and the internal and external heads are inseparable (mostly separate in _Aramus_). The origin of the scapular head is mostly from a cartilaginous pad on the humerus (entirely from the scapula in _Aramus_). The small tendinous band connecting the scapula connects first to a similar band from _M. deltoideus major_ (this intermediate attachment is lacking in _Aramus_). A small but very strong band of tendon, apparently the anchor (Berger, 1960), arises from the base of the deltoid crest and merges with a tendinous sheet on the deep side of the belly of the scapular head (no such tendon is present in _Aramus_). The connection of this head to _M. latissimus dorsi_ is much farther distal than in _Aramus_, and the attachment to the humerus is lacking here (present in _Aramus_). No ossification exists in either tendon (present in both in _Aramus_), and connection to _M. anconaeus coracoideus_ is lacking (present in _Aramus_).

Summary. This muscle is similar in all three cranes and _Aramus_, but several distinct, small specializations are found in the Rallidae. The more important of these differences

are the larger size in the rallids, the presence of a strong tendinous band that arises from the deltoid crest and is not present in the non-rallids, and the connection to the outer edge of *M. latissimus dorsi* instead of the more proximal attachment to that muscle and to the humerus in the non-rallids. The rallids agree with *G. canadensis* in the complete fusion of the internal and external heads, but these heads are mostly separate in *Aramus* and the other two cranes.

73. *M. brachialis*

Thick and entirely fleshy, short band of muscle. Located on inner side of elbow. Attaches to humerus and to ulna.

All but proximal end of belly hidden by forearm musculature. Lies ventral to proximal end of *M. extensor metacarpi radialis*, to portion of *M. supinator brevis*, and to inserting tendons of *M. biceps*. Lies dorsal to proximal ends of *M. pronator brevis* and *M. pronator longus*.

Origin. Arises mostly fleshily, but also by very small tendinous portions, from all of brachialis impression, on palmar surface of distal end of humerus.

Insertion. Attaches mostly fleshily to all of elongate brachialis impression, on palmar face of proximal end of ulna.

Action. Flexes forearm and rotates it so as to raise anterior edge of wing.

Summary. The pattern of this muscle is the typical one for birds and agrees closely in all the genera in this study.

74. *M. expansor secundariorum*

Consists of small and elongate belly composed of smooth muscle (Berger, 1956b), one short triangular aponeurosis, and a very long and very slender branched tendon. Extends along posterior edge of forearm from space posterior to coracoid to posterior edge of proximal end of forearm. Belly occupies portion of distal third of humerus. Attaches to sternum, to scapula, to *M. dorsalis scapulae*, to skin, to *M. anconaeus coracoideus*, to *M. flexor carpi ulnaris*, to secondaries, and to humerus.

Origin. Arises by two tendons. Distal origin by strong aponeurosis arising mainly from entepicondyle of humerus but partly from originating tendon of *M. flexor carpi ulnaris*. More proximal tendon arises as two very small bands, one from anterior edge of lateral remnant of dorsal manubrial spine of sternum, partly in common with fascia over intermediate part of *M. sternocoracoideus*, and another from two tiny tubercles in middle of medial face of head of scapula. Two tendons fuse in axillary region to form common tendon that passes through strong connective tissue pulley in edge of distal half of *M. dorsalis scapulae* and attaches strongly to skin as it passes distad along posterior side of upper arm. Tendon enters proximal end of belly at beginning of distal third of humerus. Proximal end of belly merges with very thin fascial sheet that lines ventral skin of metapatgium. Ventral edge of this sheet connects to tendon of proximal origin, and dorsal edge fuses with very elastic band of metapatagium and connects along with it to skin of axilla.

Insertion. Attaches to bases of calami of last five secondaries.

Action. Expands secondaries as wing is extended.

Comparisons. In the Gruidae Fisher and Goodman (1955) did not describe this muscle in _G. americana_, but it is presumably present. In _Balearica_ and _Grus_ the distal insertion has no attachment to _M. flexor carpi ulnaris_ (present in _Aramus_). In _Balearica_ and _Grus_ one branch of the proximal tendon arises from the ventral extent of the head of the scapula (arises from the middle of the inner side of the head in _Aramus_). In _Grus_ the other branch arises from the medial corner of the sternocoracoidal process of the sternum (from the lateral remnant of the dorsal spine in _Aramus_). This area was destroyed in the specimen of _Balearica_. In _Balearica_ the proximal end of the belly becomes a wide fascial sheet that attaches to the skin and continues proximad. The sheet gradually narrows to a small tendon that leaves the skin and attaches to the outer edge of the posterior part of _M. latissimus dorsi_ and follows that muscle to its insertion on the humerus. This attachment seems to be the equivalent of the attachment to the thin sheet of the metapatagium in _Aramus_, but the final attachment in the latter species is to the skin of the axilla. The insertion seems to be similar in the two cranes (and _Aramus_).

In the Rallidae the aponeurosis of the distal origin in _Rallus_ contains some fleshy tissue and is separate from, and partly deep to, the main belly. A similar condition is

present in _Fulica_, but the two bellies are more closely connected. This double condition is also mentioned by Berger (1956b) for _Gallinla chloropus_ (in _Aramus_ the distal origin is completely tendinous and intimately connected to the distal end of the single belly). _Rallus_ lacks the connection of the distal origin to _M. flexor carpi ulnaris_, but it is present in _Fulica_ (and _Aramus_). In _Rallus_, _Fulica_, and _Gallinula_ the scapular branch of the proximal tendon attaches to a tubercle on the posterodorsal corner of the inner face of the head of the scapula (inserts in the middle of the inner face of the head in _Aramus_). In both _Rallus_ and _Fulica_ the sternal attachment and the attachment of the proximal end of the belly to the patagium are as in _Aramus_. No evidence of _M. anconaeus coracoideus_ could be found associated with this muscle (the two muscles are connected in _Aramus_).

Summary. The muscle is well developed and rather similar in all three families, although its condition in _Grus americana_ is unknown. One small variation is found in the scapular attachment, which has a slightly different characteristic location for each of the three families. In _Balearica_ a unique humeral connection, by way of a fascial sheet and a tendon to _M. latissimus dorsi_, is present.

75. _M. anconaeus coracoideus_

Very minute and attenuate muscle, composed of long belly with tendon at either end. In spite of small size (48 mm x 1 mm), muscle is striated (Fürbringer, 1902). Located on

posterior side of distal third of humerus. Connects to _M_. _expansor_ _secundariorum_ and to _M_. _triceps_.

Partly deep to belly of _M_. _expansor_ _secundariorum_. Lies on superficial side of distal end of _M_. _triceps_.

Origin. Arises as small branch from tendon of proximal origin of _M_. _expansor_ _secundariorum_, about 15 mm proximal to belly of latter muscle.

Insertion. Distal end of belly gives rise to short band of tendon that inserts on tendinous sheet connecting two main tendons of _M_. _triceps_.

Action. Probably acts in adjusting position and tension of _M_. _expansor_ _secundariorum_.

Summary. The condition of the muscle agrees well in _Aramus_ and the Gruidae, although the condition in _Grus_ _americana_ is unknown. The muscle is absent in Rallidae.

76. _M_. _extensor_ _metacarpi_ _radialis_

Rather small and elongate muscle, with proximal half almost completely separated into anconal head (pars anconalis) with flattened belly and palmar head (pars palmaris) with larger, slender belly. Distal half composed of two narrow tendons that fuse at distal ends. Located on anterior edge of entire length of forearm and proximal end of hand. Attaches to humerus, to _M_. _tensor_ _patagii_ _brevis_, to _M_. _extensor_ _longus_ _digiti_ II, to _M_. _abductor_ _alae_ _digiti_ II, to _M_. _flexor_ _digiti_ II, and to metacarpal II.

Proximal half of belly of anconal head lies partly dorsal and partly distal to belly of palmar head. Muscle partly

covered dorsally by inserting tendon of _M_. _tensor patagii brevis_ and distally by inserting tendon of _M_. _tensor patagii longus_. Superficial at proximal end to part of _M_. _supinator brevis_, and at distal end, to _M_. _flexor digiti_ II. Distal end fuses to _M_. _abductor alae digiti_ II.

Origin. Anconal head arises by small, flattened tendon from proximal side of ectepicondylar prominence of distal end of humerus. Tendon extends about 3 cm and gives rise to spindle-shaped belly. Palmar head arises partly fleshily and partly by tendon; belly begins at origin. Proximal ends of two heads partially connect to each other, and both fuse to wide inserting tendon of _M_. _tensor patagii brevis_ and connect to strong fascial sheet over dorsal surface of forearm.

Insertion. Belly of anconal head ends just distal to middle of radius, giving rise to slender tendon that passes over anterodorsal face of wrist. Palmar head gives rise to ossified tendon in middle of belly. Tendon becomes exposed at distal end of belly, in middle of radius, and then passes across wrist superficial to tendon of anconal part. Tendons of two heads fuse at distal end of radius. Common tendon loses ossification, combines with tendon of _M_. _extensor longus digiti_ II, to bellies of _M_. _abductor alae digiti_ II and _M_. _flexor digiti_ II, and inserts strongly on proximal side of extensor process of metacarpal II.

Action. Extends hand.

Comparisons. In the Gruidae the palmar head in _Balearica_ extends only slightly farther distad than the proximal third

of the radius, but it is somewhat longer than in either species of *Grus* (in *Aramus* it extends the entire proximal half of radius). In none of the three cranes does the anconal head extend distad quite as far as the middle of the radius (in *Aramus* it extends slightly beyond the middle). In *Balearica* (and *Aramus*) both heads are connected to the insertion of *M. tensor patagii brevis*, but in both species of *Grus* this connection is only to the anconal head. The anconal part in *Balearica* (and *Aramus*) arises by one tendon, but usually by two in *Grus*. In *Balearica* and *G. americana* the tendons of both heads are ossified, but Berger mentioned ossification only in the common inserting tendon in *G. canadensis* (in *Aramus* only the tendon from the palmar head is ossified). In *Balearica* (and *Aramus*) the insertion is connected to *M. extensor longus digiti* II and to *M. abductor alae digiti* II. Apparently in *Grus* there is connection to the former but not the latter muscle (in *Aramus* the muscle has additional fusion to *M. flexor digiti* II).

In the Rallidae the separation of the two heads in *Rallus* is variable, and on the basis of three specimens, larger birds have a separation comparable to that of *Aramus* and smaller ones have the two heads completely fused. In *Fulica* the two heads are largely separate (as in *Aramus*). In both rallids the anconal head is longer and wider than in *Aramus*. In both rallids the anconal head is longer and wider than in *Aramus*. In both rallids the two heads have a common origin (partly separate in *Aramus*). In *Rallus* the length of the

bellies is variable, occupying from two-thirds to three-quarters of the length of the radius. In Fulica the length is constant and slightly less than the shortest length in Rallus(but still longer than in Aramus). In Rallus the inserting tendon may be single or double, according to the degree of fusion of the bellies, but in Fulica (as in Aramus) two tendons are always present. No ossification of the tendons occurs in either rallid (the palmar tendon is ossified in Aramus). In both rallids the insertion is similar to the one in Aramus, except for lacking connection to M. flexor digiti II and in being covered by the cartilaginous pad of the insertion of M. tensor patagii longus.

Summary. The fleshy portion of the muscle is longest in Rallidae, intermediate in Aramidae, and shortest in Gruidae. The anconal head is smaller in the limpkin and the gruids than in the rallids. Both inserting tendons are ossified in the cranes, only one is in Aramus, and neither is ossified in the rallids. The number of muscles connecting to the insertion is variable among the groups. Rallus is unique in having individual variation in the separation of the two heads.

77. M. extensor digitorum communis

Small muscle with very elongate, partly bipinnate belly that has triangular cross section and tapers to point at both ends. At middle of radius distal end of belly becomes long, slender tendon that branches distally. Runs along postero-dorsal surface of radius and anterodorsal edge of hand.

Attaches to humerus, to *M. supinator brevis*, to *M. anconeus*, to digit II, and to phalanx 1 of digit III.

Proximal end fused to posterior edge of *M. supinator brevis*. Lies superficial to anterior edge of *M. anconeus* along anterior edge of *M. flexor metacarpi radialis* for full length of forearm. Connects fleshily to latter two muscles. See insertion.

Origin. Arises partly from proximal region of ectepicondylar prominence of humerus by small tendon partly in common with *M. supinator brevis* and just proximal to origin of *M. anconeus*. Tendon immediately becomes wider and fleshy and receives fleshy origin from elongate area occupying most of proximal half of posterodorsal face of radius and receives another from anterior edge of proximal half of *M. anconeus*.

Insertion. At its distal end belly gives rise to very slender tendon, ossified along radius, that passes over wrist through separate connective tissue loop on dorsal face of external condyle of ulna. Tendon passes along anterodorsal edge of *M. flexor metacarpi posterior* and onto metacarpal III, passes over tendon of *M. extensor longus digiti* III and over tendon of branch that passes between *M. extensor brevis digiti* II and *M. abductor alae digiti* II. Attaches onto posterodorsal edge of digiti II (pollex), about 4 mm from proximal end of that bone; main tendon continues for length of hand, passes under tendon of *M. extensor longus digiti* III and through fibrous pulley, makes a sharp turn anteriad, passes back under latter tendon, and inserts on

anterodorsal face of proximal edge of phalanx 1 of digit III.

Action. Extends hand and adducts alula.

Comparisons. In the Gruidae the distal end of the belly in *Balearica* and *G. americana* arises slightly less than half way out on the radius, but in *G. canadensis* it extends only slightly beyond the proximal third (ends in *Aramus* just distal to the middle of the radius). In *Balearica* the muscle arises fleshily from less than one-fifth of the length of the radius, but from about one-third in *G. americana* (from about one-fourth in *Aramus*). This origin is undescribed but probably very small in *G. canadensis*. In *G. americana* the origin is in common with *M. anconeus* (unknown for *G. canadensis*) but is essentially separate in *Balearica* and *Aramus*. In *Balearica* (and *Aramus*) the inserting tendon is ossified, but this character is not mentioned for *Grus*. In some specimens of *G. americana* one branch of the inserting tendon attaches to metacarpal II, but this branch is lacking in some members of that species as well as in the other two cranes (and *Aramus*). In *Balearica* (and *Aramus*), but apparently not in *Grus*, the extreme distal end of the main tendon makes an abrupt turn anteriad to pass again under the tendon of *M. extensor longus digiti* III.

In the Rallidae the length of the belly in *Rallus* varies between slightly more than half the length of the radius in smaller specimens, to nearly two-thirds the length in larger birds. In *Fulica* the belly occupies the proximal three-quarters of the radius (in *Aramus* it extends for only half

the radius. In Rallus the main origin is more strongly connected to M. anconeus than in Fulica (or Aramus). In both rallids the fleshy origin is much smaller than in Aramus, and may even be lacking in Rallus. In Rallus there is additional fleshy origin from M. supinator brevis, and in Fulica there is weak fascial connection to M. anconeus (neither is present in Aramus). In both rallids the tendon is soft (ossified in Aramus), and it passes the wrist through a stronger loop than in Aramus. In Rallus the tendon to digit II attaches in the center of the bone but inserts nearer the proximal end in Fulica (and Aramus). In Fulica, but not in Rallus (or Aramus), a small branch of the tendon to digit II connects strongly to connective tissue associated with the bases of the alular feathers.

Summary. The muscle agrees in general in each genus studied, but distinct small variations are present. The length of the belly is different in each genus and even among individuals of Rallus, but it is generally longest in Rallidae, intermediate in Aramus, and shortest in Gruidae. The fleshy origin from the radius is variable but is larger in the limpkin than in the gruids or the rallids. Small extra branches of the inserting tendon occur in Fulica and in some specimens of Grus americana. Ossification of the proximal portion of the inserting tendon is found in Aramus and Balearica, but it is not mentioned for Grus and is absent in the rallids.

78. *M. supinator brevis*

Small and flattened muscle with pinnate belly, fusiform in anterior view. Located on anterior side of proximal end of forearm. Attaches to humerus, to *M. extensor digitorum* communis, to *M. pronator brevis* and to radius.

Lies posterior to belly of *M. extensor metacarpi radialis* and ventral to and fused with edge of belly of *M. extensor digitorum communis*. Proximal end dorsal to *M. brachialis*, and whole belly lies anterodorsal to *M. pronator brevis*.

Origin. Arises tendinously, in common with *M. extensor digitorum communis*, from ectepicondylar prominence of humerus.

Insertion. Belly arises almost at origin and immediately begins to insert fleshily on joint ligaments and on anterior face of proximal two-fifths of radius; also inserts fleshily on anterior edge of *M. pronator brevis*.

Action. Flexes forearm on humerus and rotates anterior edge of wing upward.

Comparisons. In the Gruidae the muscle in *Balearica* (and *Aramus*) extends over the proximal two-fifths of the radius, but it is shorter in *Grus*, being from one-fourth to one-third the length of the radius in *americana* and one-third the length in *canadensis*. In *Balearica* (and *Aramus*) the anteroventral edge of the belly is fused with *M. pronator brevis*, but this attachment is apparently lacking in *Grus*.

In the Rallidae the belly is a little longer than in *Aramus*, and it is slightly longer in *Rallus* than in *Fulica*. In *Rallus* the origin is in common with *M. anconeus* as well

as _M. extensor digitorum communis_, but in _Fulica_ (and _Aramus_) its origin is connected only with the latter muscle. The insertion in both rallids is more on the dorsal face of the radius, and it is rounded at the anterior end (in _Aramus_ it is more on the anterior face of the radius and is attenuated at the anterior end). In both rallids (as in _Aramus_) the muscle connects to _M. pronator brevis_.

Summary. The length of the belly is variable, being longest in the two rallids, intermediate in _Aramus_ and _Balearica_, and shortest in _Grus_. The insertion in the Rallidae is located more to the dorsal side of the radius than in _Aramus_ and the Gruidae. No connection of the muscle to _M. pronator brevis_ is mentioned for _Grus_, but a strong attachment to this muscle is found in _Balearica_ and the non-gruids. The general configuration of this small muscle is essentially similar in all three families.

79. _M. flexor metacarpi radialis_

Very narrow muscle with band-like proximal tendon connected to slender distal tendon by elongated bipinnate belly. Runs in middle of full length of dorsal side of forearm. Attaches to humerus, to _M. extensor digitorum communis_, to _M. anconeus_, and to metacarpal III.

Lies anterior and partly superficial to _M. anconeus_ and runs along posterior edge of _M. extensor digitorum communis_, and fuses to both muscles. Partly superficial to _M. extensor longus digiti_ II. Strong vinculum arises from proximal

portion and passes posteriad to attach to skin and posterior edge of proximal end of ulna.

Origin. Arises from external face of ectepicondyle of humerus, by strong, partly ossified aponeurosis that is common to proximal third of *M. anconeus*. Tendon becomes free and gives rise to belly about one-sixth of way out forearm. In middle of forearm muscle has fleshy origin from distal third of *M. anconeus*.

Insertion. Wide ossified tendon begins to form in middle of forearm; tendon narrows and becomes free of belly in distal sixth of forearm. Tendon passes through tendinal groove on external condyle of ulna in unossified condition, and inserts on minute intermetacarpal tuberosity, which lies on posterodorsal edge of metacarpal III just distal to beginning of intermetacarpal space.

Action. Flexes hand and forearm (see Gadow, 1893).

Comparisons. In the Gruidae the origin in *Balearica* and *G. canadensis* is in common with *M. anconeus* (this connection is more extensive in *Aramus*), but the muscle arises separately in *G. americana*. In *Balearica* (and *Aramus*) there is fleshy origin from the distal portion of *M. anconeus*, but this is not mentioned for *Grus*. In *Balearica* the belly extends only for three-quarters of the length of the forearm, but in *Grus* (and *Aramus*) it extends for five-sixths. The tendon of insertion is ossified in *Balearica* and *G. canadensis* (and *Aramus*), but the condition is unknown for *G. americana*. The insertion is on the small intermetacarpal process, which

in Balearica and G. canadensis is minute and located on metacarpal III, just proximal to the intermetacarpal space, but in G. americana the insertion is on the fused area of metacarpals III and IV (in Aramus the tubercle is also minute but located just distal to the beginning of the space).

In the Rallidae the muscle in Rallus arises by a narrow tendon that has only weak connection to M. anconeus, but in Fulica (and Aramus) this tendon is wider and fused to M. anconeus. In Rallus the fleshy origin from the distal end of M. anconeus is lacking, but is present in a very small area in Fulica (larger in Aramus). In both rallids the belly extends nearly to the wrist (but it is shorter in Aramus). In Rallus the insertion is on a facet at the level of the proximal portion of the intermetacarpal space (similar in Aramus), but in Fulica this facet is proximal to the space. Neither rallid has ossification of the inserting tendon (present in Aramus).

Summary. Only small variations are found among the three families. The main origin is similar in all genera except Rallus, in which the tendon is much narrower and more independent. The fleshy origin from M. anconeus is absent only in Grus americana and Aramus. The belly of the muscle is about equal in the cranes and the limpkin, but it is longer in the rallids. The tendon of insertion is variable, having the most proximal location in Grus americana and Fulica, an intermediate one in Grus canadensis and Rallus, and the most distal location in Aramus.

80. *M. pronator brevis*

Rather small muscle with flat and elongately oval belly. Lies on ventral side of proximal portion of forearm, from elbow joint to anterior edge of radius. Attaches to humerus, to *M. supinator brevis*, to *M. pronator longus*, and to radius.

Lies posterior to belly of *M. extensor metacarpi radialis*, and proximal portion lies anterior to part of belly of *M. flexor carpi ulnaris*. Anterior edge connected to anterior edge of *M. supinator brevis*. Superficial to most of belly of *M. pronator longus* and connected to anterior edge, and superficial to portion of belly of *M. brachialis*.

Origin. Arises by rounded tendon from proximal portion of entepicondyle of humerus; tendon immediately widens into belly.

Insertion. Inserts by thin aponeurosis onto slightly more than second fifth of anteroventral edge of radius. Connected to insertions of *M. pronator longus* and *M. supinator brevis*.

Action. Flexes forearm and rotates anterior edge of wing downward.

Comparisons. In the Gruidae the muscle extends for about the proximal third of the forearm, or slightly less (in *Aramus* it extends for about two-fifths of the forearm). In all three cranes the tendon of origin is flat, and the insertion is in about the second sixth of the forearm (in *Aramus* the tendon of origin is round, and the insertion is in about the second fifth of the forearm). In *Balearica* (and *Aramus*)

the muscle connects to _M_. _supinator brevis_ and _M_. _peroneus longus_, but these contacts are not mentioned for _Grus_.

In the Rallidae the muscle extends for about half the forearm (for only two-fifths of the forearm in _Aramus_). In both _Rallus_ and _Fulica_ the tendon of origin is small but flattened (small and rounded in _Aramus_). Neither rallid has connection of this muscle to surrounding muscles (in _Aramus_ it connects to adjacent muscles).

Summary. The muscle is shortest in the cranes, of intermediate length in _Aramus_, and is longest in the rallids. The tendon of origin is rounded in _Aramus_, but in both Gruidae and Rallidae it is flattened. There are seemingly insignificant variations in attachments of this muscle to surrounding ones.

81. _M_. _pronator longus_

Medium-sized muscle with flat but thick belly. Lies on ventral side of proximal half of forearm. Attaches to humerus, to _M_. _pronator brevis_, to _M_. _extensor longus digiti_ II, to _M_. _extensor longus digiti_ III, and to radius.

Most of belly deep to _M_. _pronator brevis_, and lies partly deep to anterior edge of _M_. _flexor digitorum sublimus_. Superficial to portion of _M_. _brachialis_, to belly of _M_. _flexor digiti profundus_, to posterior portion of _M_. _extensor longus digiti_ III, to anterior portion of _M_. _extensor longus digiti_ II, and to anterior edge of belly of _M_. _flexor digitorum profundus_; connected to latter two muscles and to _M_. _pronator brevis_.

Origin. Arises by small, rounded tendon from distal portion of entepicondyle of humerus, partly deep to origin of _M_. _flexor carpi ulnaris_; tendon immediately widens into belly.

Insertion. Attaches by mixed fleshy and tendinous fibers to second and third fifths of ventral face of radius, to anterior edge of ventral surface of belly of _M_. _extensor longus digiti_ II, and to proximal portion of ventral surface of _M_. _extensor longus digiti_ III.

Action. Flexes forearm and depresses anterior edge of wing.

Comparisons. In the Gruidae the belly in _Balearica_ and _G_. _americana_ extends for about the proximal third of the forearm, and in _G_. _canadensis_ "less than half way down the forearm" (Berger, 1956a) (in _Aramus_ the muscle extends for three-fifths of the forearm). In all three cranes the originating tendon is wide and flattened, (rounded in _Aramus_). In _Balearica_ (and _Aramus_) the insertion is partly on some adjacent muscles, but in _Grus_, it is apparently only on the radius. In none of the three cranes does the belly extend anteriad far enough to insert on _M. extensor longus digiti_ III (inserts partly on that muscle in _Aramus_).

In the Rallidae the length of the muscle in _Rallus_ varies from about two-thirds of the forearm in small specimens to four-fifths in larger ones. In _Fulica_ the belly extends for five-sixths of the forearm (in _Aramus_ it extends for only three-fifths of the forearm). In both rallids a small and fleshy, partially-separate portion, which sometimes arises

separately in _Rallus_, is present on the anterior edge of the proximal end. This portion (not present in _Aramus_) is not enclosed in the fascia of the main part. In both rallids the originating tendon is only slightly flatter than in _Aramus_, and (like _Aramus_) the insertion is partly on _M. extensor longus digiti_ III.

Summary. The belly of the muscle is quite short in Gruidae, long in _Aramus_, and very long in Rallidae. The tendon of origin is rounded in _Aramus_, somewhat flattened in Rallidae, and wide and quite flat in Gruidae. _Aramus_ agrees with Rallidae in having the insertion located far enough distally to attach to _M. extensor longus digiti_ III.

82. _M. extensor longus digiti_ II

Small bipinnate muscle with flat, triangular belly, attenuated into long, slender tendon at distal end. Located between radius and ulna in proximal half of forearm, but tendon extends along ulna to hand. Attaches to ulna, to radius, to _M. pronator longus_, to _M. flexor digitorum profundus_, to _M. extensor metacarpi radialis_, and to metacarpal II.

Covered ventrally by _M. pronator longus_ and _M. brachialis_ and dorsally by _M. anconeus_ and by _M. extensor digitorum communis_. Connects to anterior edge of belly of _M. flexor digitorum profundus_.

Origin. Arises partly by mixed fibers from narrow line on anteroventral edge of ulna, from joint ligaments throughout proximal third of bone, between origins of _M. flexor digitorum profundus_ and _M. anconeus_. Originates also by

fleshy fibers from all but distal fourth of radius, loosely from posterior face of proximal half and more strongly from posterodorsal face of more distal portion; arises also by fleshy from anterior edge of belly of M. pronator longus.

Insertion. Ossified tendon begins to form within belly in middle of forearm, becomes free as slender, flattened tendon in distal sixth of forearm, runs along posterodorsal edge of radius, and passes through tendinal groove of radius. Distal to wrist tendon fuses with tendon of M. extensor metacarpi radialis and inserts in common with it, but on dorsal face of extensor process of metacarpal II.

Action. Extends hand.

Comparisons. In the Gruidae, Balearica has the belly extending through all but the distal eighth of the forearm, but in Grus it occupies only from one-half to two-thirds of the radius (in Aramus it occupies five-sixths of the radius). In all three cranes the origin begins just distal to the insertion of M. biceps (in Aramus it begins on the ligaments of the elbow joint). In Balearica (and Aramus) the origin is partly from M. flexor carpi ulnaris brevis and M. pronator longus, but these connections apparently are lacking in Grus. Ossification of the inserting tendon is not mentioned for G. americana, but is found in the other two cranes (and Aramus). The insertion is quite similar in all three cranes (and Aramus).

In the Rallidae the belly extends distad to the expanded distal end of the radius (in Aramus it is shorter, extending

only through the proximal five-sixths of the radius). In both rallids the proximal end of the origin is from the area of the tendon of *M. biceps* (from the elbow joint in *Aramus*). In neither rallid is there ossification in the inserting tendon (present in *Aramus*).

Summary. The belly of the muscle is very long in *Balearica* and the rallids, intermediate in *Aramus*, and shortest in *Grus*. The origin begins farther proximally in *Aramus* than in Gruidae or Rallidae, and in each genus (except perhaps *Grus*) the muscle also arises from some surrounding muscles. The tendon of the insertion is ossified in *Aramus* and Gruidae (uncertain for *G. americana*), but is not in Rallidae. The insertion agrees well in all three families.

83. *M. anconeus*

Very elongated triangular muscle, with belly rather thick and partially bipinnate. Dorsal face covered with silvery and partially ossified aponeurosis. Located inside posterior edge of proximal half of forearm. Attaches to humerus, to ulna, to *M. flexor metacarpi radialis*, to *M. extensor digitorum communis*, to *M. flexor carpi ulnaris brevis*, to *M. flexor digitorum profundus*, and indirectly to skin.

In dorsal view anterior edge deep to and attached to posteroventral side of *M. extensor digitorum communis*, and portion of middle of belly deep to *M. flexor metacarpi radialis*. Posterior to *M. supinator brevis*. Superficial in dorsal view to most of *M. extensor longus digiti* II, part of *M. peroneus longus*, and to connected belly of *M. flexor digitorum profundus*.

Origin. Arises in common with M. flexor metacarpi radialis by strong, flat tendon from external face of ectepicondyle of humerus, just distal to origin of M. extensor digitorum communis. Tendon widens into belly at proximal end of ulna.

Insertion. Inserts fleshily on posterior face of proximal two-thirds of ulna, beginning just distal to elbow joint. Superficial fascia over belly continuous with vinculum of M. flexor metacarpi radialis, attaching to ulna and to skin. Ventral edge of anterior extent of insertion fuses with M. flexor carpi ulnaris brevis.

Action. Flexes forearm.

Comparisons. In the Gruidae the muscle extends for about half the ulna (in Aramus it is two-thirds the length of the ulna). In Balearica and G. canadensis the origin is partly in common with M. flexor metacarpi radialis (extensively so in Aramus), but it arises independently in G. americana. In Balearica, (and Aramus) but apparently not in Grus, the ventral aspect of the muscle is connected to M. flexor digitorum profundus, and the anterior, distal portion connects to M. flexor carpi ulnaris brevis; the attachment to M. supinator brevis (present in Aramus) is lacking in all three cranes.

In the Rallidae the muscle shows individual variation. In both genera the belly extends for at least three-quarters of the ulnar length, but in the largest specimens of Rallus it is four-fifths that length, and in Fulica it may be as long as five-sixths (in Aramus it is rather constant at

about two-thirds the length of the ulna). In Rallus, but not in Fulica (or Aramus), the origin is partly in common with M. supinator brevis. In Rallus the origin is nearly independent of M. flexor metacarpi radialis, but in Fulica (and Aramus) the two muscles are inseparable at their origins. In both rallids the deep aspect of the muscle has extensive connection to M. flexor digitorum profundus (less extensive in Aramus).

Summary. The muscle differs mainly in the length of the belly among the three families. The length is least in the cranes, intermediate in Aramus, and greatest in the rallids. In only the Rallidae is there obvious individual variation, and it is correlated with size in Rallus. The origin is extensively connected to M. flexor metacarpi radialis in Aramus and Fulica and to lesser degree in Balearica, but in Grus and Rallus the two origins are essentially independent. Connections to other muscles are apparently also variable among the genera.

84. M. extensor longus digiti III

Very small muscle with slender belly extending to wrist. Long and narrow ossified tendon arises from distal end of somewhat pinnate belly. Located along posterior side of distal half of radius, but tendon passes onto dorsal side of hand. Attaches to radius, to M. pronator longus, to M. flexor metacarpi brevis, and to phalanges 1 and 2 of digit III.

In dorsal view, lies deep to M. extensor longus digiti II. In ventral view deep to anterior end of M. pronator longus

and to heavy fascial sheet from _M_. _flexor carpi ulnaris_. Anterior to _M_. _flexor carpi ulnaris brevis_ and anteroventral to _M_. _flexor metacarpi radialis_.

Origin. Attaches to posterior face of whole distal half of radius, but arises mainly by fleshy and tendinous fibers from posterior edge of fourth sixth, and attaches only weakly to more distal portion of radius; arises also from distal end of _M_. _pronator longus_.

Insertion. Tendon passes through tendinal groove between condyles of ulna and then branches just beyond wrist. In proximal half of dorsal face of hand, tendon passes under tendon of _M_. _extensor digitorum communis_, connects strongly to tendons associated with bases of most proximal primaries, and receives inserting tendon of _M_. _flexor metacarpi brevis_. In center of metacarpal III tendon passes over tendon of _M_. _extensor digitorum communis_ and under tendons from primaries, then attaches strongly to proximal end of phalanx 1 of digit III and continues on to insert strongly on proximal end of phalanx 2 of digit III.

Action. Extends digit III.

Comparisons. In the Gruidae the belly in _Balearica_ and _G_. _americana_ (as well as _Aramus_) is located on the distal half of the radius, but in _G_. _canadensis_ it occupies the distal two-thirds. In _Balearica_ and _G_. _canadensis_ it originates from the whole distal half of the radius. In _G_. _americana_ the origin is from the middle third (in _Aramus_ it arises from the distal half, but strongly only from the

fourth sixth). In *Balearica* (and *Aramus*) a portion of the origin is from *M. pronator longus*, and the proximal portion of the inserting tendon is ossified and connects to tendons associated with primaries and to *M. flexor metacarpi brevis*. In *Grus* the above three connections are absent, and there is no ossification. In *Balearica* (and *Aramus*) there is a proximal insertion, on phalanx 1 of digit III, that is not present in *Grus*.

In the Rallidae the only difference between the two genera is that in *Fulica* the belly is slightly longer, extends farther distad, and has a somewhat longer origin than *Rallus*. In both rallids the belly is somewhat longer than half the length of the radius and extends to the distal end of the forearm. In both *Rallus* and *Fulica* the connection to *M. pronator longus* is longer than in *Aramus*, the tendon of insertion is unossified (ossified in *Aramus*), and it is not connected to *M. extensor metacarpi brevis* (the latter muscle inserts on the tendon in *Aramus*). In both rallids (as in *Aramus*) the inserting tendon connects to tendons associated with primaries and attaches to the proximal end of digit 1. In the other two rallids it also attaches by a branch to the distal end of metacarpal III (this connection is absent in *Aramus*).

Summary. The length of the belly is about equal in *Aramus* and *Balearica*, slightly longer in the rallids, and considerably longer in *Grus*. The extend of the origin is variable among the genera. The origin from *M. pronator longus*

is lacking only in _Grus_. Connection to _M. flexor metacarpi brevis_ is present in _Aramus_ and _Balearica_, absent in _Grus_ and Rallidae. The connection to tendons of the primaries and the insertion on phalanx 1 are lacking only in _Grus_. In Rallidae there is an additional insertion, on the distal end of metacarpal III, that is absent in _Aramus_ and Gruidae.

85. _M. flexor digitorum profundus_

Small and very elongate muscle, with full length of belly strongly bipinnate and notched at proximal end. Distal end attenuated, giving rise to elongate tendon. Attaches to ulna, to _M. extensor longus digiti_ II, to _M. anconeus_, to _M. flexor carpi ulnaris brevis_, and to phalanx 2 of digit III.

Most of belly deep to _M. flexor digitorum sublimus_, but also to posterior edge of _M. pronator longus_. _M. brachialis_ fits into notch in distal end. Adjacent and connected to posterior edges of origin of _M. extensor longus digiti_ II and insertion of _M. anconeus_. Connected to, and partly superficial to, posterior end of _M. flexor carpi ulnaris brevis_.

Origin. Main origin mostly fleshy from irregular area on ventral face of proximal end of ulna, extending from distal edge of anterior ligamental prominence (Howard, 1929) and along posterior edge of brachialis impression to become wider in area between impression and proximal end of insertion of _M. flexor carpi ulnaris brevis_. Arises also partly from latter muscle, from posterior edges of _M. extensor longus digiti_ II, and from _M. anconeus_.

Insertion. Slightly ossified, narrow tendon forms within distal third of belly and extends along *M. flexor carpi ulnaris brevis* to pass across ventral face of wrist under two strong ligamentous bands. Passes over anterior side of pisiform process of carpometacarpus, under belly of *M. flexor digiti* II, along length of ventral side of belly of *M abductor major digiti* III, and along anteroventral edge of phalanx of digit III, in contact with tendon of anterior part of *M. flexor carpi ulnaris*. At distal end of phalanx 1, tendon turns inward to insert on anteroventral corner of proximal end of phalanx 2 of digit III.

Action. Extends and depresses digit III and flexes hand.

Comparisons. In the Gruidae the belly in *Balearica* extends for about the proximal half of the forearm, but it extends for less than half the forearm in *Grus* and for only about two-fifths of the forearm in *G. americana* (belly occupies two-thirds of the forearm in *Aramus*). In *Balearica* and *G. canadensis* (and *Aramus*) the proximal end of the belly is notched, but it seems to be pointed and entire in *G. americana*. In *Balearica* (and *Aramus*) the origin extends distad halfway out the forearm and arises partly from *M. extensor longus digiti* II and from *M. anconeus*. In *Grus* it extends only one-third of the way out and does not arise from those two muscles. In *Balearica* and *G. canadensis* the tendon is ossified both proximal and distal to the wrist (ossified only in the proximal portion in *Aramus*). This character is not given for *G. americana*.

In the Rallidae the muscle is large, extending nearly the full length of the forearm, and the belly is not notched proximally and is thickest in its distal half, with a rather rounded distal end (in _Aramus_ the belly extends for two-thirds of the forearm, is notched, and the distal end is smaller and attenuated). In both _Rallus_ and _Fulica_ the origin is from a longer area of the radius, the attachment to _M_. _flexor_ _carpi_ _ulnaris_ _brevis_ is stronger, and the origin from _M_. _anconeus_ is more extensive, than in _Aramus_. In the two rallids the inserting tendon is ossified only in the portion distal to the wrist, and the tendon connects to _M_. _abductor_ _major_ _digiti_ III (in _Aramus_ the tendon is ossified only proximal to the wrist, and it does not attach to the latter muscle). In _Rallus_, but not in _Fulica_ (or _Aramus_), the tendon sometimes penetrates the tendon of _M_. _flexor_ _carpi_ _ulnaris_ at the distal end of digit 1.

Summary. This muscle in rallidae is quite significantly distinct from its representatives in _Aramus_ and Gruidae, mainly in being much longer and thicker in the rails. Connections to _M_. _extensor_ _longus_ _digiti_ II and _M_. _anconeus_ are lacking only in _Grus_. In _Rallus_ alone, the tendon sometimes penetrates another one. Ossification of the tendon is variable; it is ossified in the proximal and distal portions in _Balearica_ and _G_. _canadensis_ (not mentioned for _G_. _americana_), but only in the distal portion in the rallids.

86. _M. flexor digitorum sublimus_

Elongate, rudimentary muscle composed partly of deep, bipinnate belly and partly of wide, superficial, tendinous band extending full length of forearm. Located in posterior half of ventral side of forearm. Attaches to humerus, to ulnare, and to phalanx 2 of digit III. Connects indirectly to _M. flexor carpi ulnaris_, to secondaries and greater ventral coverts, and to ulna.

The muscle is considered by Fisher and Goodman (1955) and by Fisher (1946) as the anterior part of _M. flexor carpi ulnaris_.

Belly partly superficial and partly anterior to _M. flexor carpi ulnaris_, to _M. flexor digitorum profundus_, and to _M. flexor carpi ulnaris brevis_. Origin partly superficial to origin of _M. pronator longus_.

Origin. Arises by strong, thick tendon from rounded facet on distal, anconal corner of entepicondyle of humerus. Tendon passes down forearm, widening and folding over anterior edge of _M. flexor carpi ulnaris_. Bipinnate belly arises fleshily from deep side of tendon, beginning proximally where tendon begins to fold and ending distally about two-thirds of the way out forearm. At point of origin from humerus, tendon connects by fascial sheet to origin of _M. flexor carpi ulnaris_ and its associated joint ligament.

Insertion. Wide, superficial tendon becomes smaller and more compact and divides at elbow. One branch inserts strongly on line on anterior face of ulnare, near ventral edge,

and second branch merges with wide connective tissue sheet covering posterior portion of ventral surface of hand. An aponeurosis extends posteriad from full length of tendon, to merge with aponeurosis from _M. flexor carpi ulnaris_. Ossified tendon forms within belly, and becomes detached from wide tendon in distal extent. Belly ends about 5 mm from wrist, but tendon passes in unossified condition between two branches of superficial tendon and through fibrous canal at antero-distal corner of ulnare, again becomes ossified and passes along ventral side of belly of _M. abductor major digiti_ III in contact with tendon of _M. flexor digitorum profundus_, passes under latter tendon, and continues distad to insert strongly on entire anteroventral edge of phalanx 2 of digit III.

Action. Wide, superficial tendon holds wing in extended position. Long tendon extends hand, and attachment to secondaries seems to serve as pivot, on which feathers are expanded as arm is extended.

Comparisons. In the Gruidae the entire length of the superficial aponeurosis in _Balearica_ and _Aramus_) connects to the ulna and to the secondaries, but in _G. americana_ (and perhaps in _G. canadensis_) only the proximal half is so connected. In _Balearica_ and _G. canadensis_ (as well as in _Aramus_) the small tendon from the belly passes the wrist without fusing with the main, superficial tendon; in _G. americana_ the two tendons are partly fused. In _Balearica_ and _G. canadensis_ the small tendon is ossified in portions both

proximal and distal to the wrist (in *Aramus* it is ossified only distal to the wrist). The condition in *G. americana* is unknown.

In the Rallidae the belly is wider and extends farther distad than in *Aramus*. In both rallids the tendon from the belly has no ossification (ossified in distal portion in *Aramus*), passes over ventral face of ulnare (over anterior edge in *Aramus*), and inserts on the distal end of phalanx 1 of digit III (in *Aramus* the insertion is on the full length of phalanx 2). Sometimes in *Rallus* the tendon may be penetrated by the tendon of *M. flexor digitorum profundus*.

Summary. *Aramus* agrees with the cranes in having ossification of the long tendon, in having it pass anterior to the ulnare, and in having the insertion on phalanx 2. In the rallids there is no ossification, the tendon passes ventral to the ulnare, and the insertion is significantly different, on phalanx 1. Other features of the muscle are quite similar in the three families.

87. *M. flexor carpi ulnaris*

Elongate muscle with two partially separate bellies. Lies on posterior portion of ventral surface of forearm. Attaches to humerus, to humero-ulnar pully, and to ulnare. Connects indirectly to *M. flexor digitorum sublimus*, to ulna, to secondaries, and to major ventral coverts.

Partly deep and partly posterior to *M. flexor digitorum sublimus*. Partly superficial to *M. pronator longus*, to *M. flexor digitorum profundus*, and to *M. flexor carpi ulnaris brevis*.

Origin. Arises from palmar face of entepicondyle of humerus, in common with joint ligament connecting entepicondyle and olecranon process. Ligament forms loop (humero-ulnar pully) around tendon and connects to aponeurosis over elbow and indirectly to _M. expansor secondariorum._ Tendon separates from ligament, passes through loop, widens, and immediately gives rise to set of fleshy bundles on each side. About one-third way out forearm, deeper and more posterior belly separates, and tendon of origin continues distad for two-thirds of forearm, enclosed within superficial belly and forming basis of its bipinnate structure.

Insertion. Superficial belly forms ossified tendon superficially along anterior edge. Anteriorly tendon becomes thickly rounded, but looses ossification and inserts strongly onto ventral aspect of proximal face of ulnare, along with some fleshy fibers of anterior extent of belly. Deeper, more posterior belly continues posteriod as fascial sheet that merges with similar sheet from _M. flexor digitorum sublimus_. Common sheet forms series of triangular projections, each of which attaches to calamus of one secondary, to tip of one greater ventral covert, and to adjacent spot on ulna. Belly ends in middle of ulnar length, at which point small tendon arises in aponeurosis and continues distad to insert on ventral corner of proximal end of ulnare, just ventral to insertion of superficial belly.

Action. Flexes forearm and hand. Action involved in attachment to secondaries same as for _M. flexor digitorum sublimus_.

Comparisons. In the Gruidae the superficial belly is small and located mostly in the proximal third of the forearm (much larger in Aramus and well developed all the way to the wrist). Both the humero-ulnar pulley associated with the origin and the ossification in the tendon of the superficial belly are present in Balearica and G. canadensis (as well as Aramus), but neither is mentioned for G. americana. In Balearica and G. canadensis (and Aramus) a well developed tendon arises from the distal end of the deep belly and inserts near the attachment of the tendon of the superficial belly. This insertion is not mentioned for G. americana.

In the Rallidae the superficial belly is well developed but narrow, and the deep belly extends nearly to the wrist (in Aramus the superficial belly is wider, but the deep belly is much shorter). In the rails the two bellies are closely connected throughout (in Aramus they are partly separate). In Rallus the insertions of the two tendons may be separate (as in Aramus), or the deep one may branch and insert only partly separately. In Fulica the tendons fuse at their distal ends and insert together. No ossification is present in the superficial tendon in either rallid (present in Aramus).

Summary. The superficial belly is best developed in Aramus, is of intermediate size in Rallidae, and smallest in Gruidae, but the deep belly is larger in the rallids than in either Aramus or the cranes. Aramus agrees with Gruidae in having some separation of the two bellies and differs from Rallidae, in which the two are thoroughly fused. The insertion is slightly variable in both the cranes and the rails.

88. *M. flexor carpi ulnaris brevis*

Elongate, but somewhat widely flattened muscle, extending for short distance distally as small tendon. Located on ventral surface of distal half of ulna. Attaches to ulna, to *M. anconeus*, and to carpometacarpus.

Deep to parts of *M. flexor digitorum profundus*, to *M. flexor digitorum sublimus*, to *M. flexor carpi ulnaris*, and to *M. pronator longus*. Adjoins anteroventral edge of *M. anconeus* and lies posterior to distal end of *M. extensor longus digiti* III.

Origin. Arises fleshily from ventral surface of most of distal half of ulna, beginning at anterior edge of origin of *M. flexor digitorum profundus*.

Insertion. Ossified tendon forms superficially down middle of distal two-thirds of belly. Belly ends just proximal to wrist, but tendon proceeds distad, loses ossification, passes under ligament joining distal end of radius with pisiform process of carpometacarpus, and over ventral face of radiale. Tendon then becomes more widely flattened, turns dorsad across proximal end of carpometacarpus, passes under tendons of *M. tensor patagii longus*, *M. extensor longus digiti* II, and *M. extensor metacarpi radialis*, and inserts on oval scar on anterior edge of dorsal (external) carpal trochlea.

Action. Capable of flexing hand if wing is completely extended (Fisher, 1946). Rotates hand so as to depress anterior edge of distal portion of wing.

Comparisons. In the Gruidae the belly and its origin are narrow and do not cover the full width of the ulna (in _Aramus_ the belly covers the whole ventral surface of the ulna in the region of origin). In _Balearica_ (and _Aramus_) the origin occupies the distal half of the ulna, but _G. americana_ it arises from the distal two-thirds, and from slightly more than the distal half in _G. canadensis_. In _Balearica_ the portion of the tendon proximal to the wrist is very strongly ossified (in _Aramus_ it is also well ossified), but this condition is not mentioned for _Grus_. In _Balearica_ (and _Aramus_) the proximal portion of the belly is fused with _M. anconeus_, but the two muscles are apparently separate in _Grus_.

In the Rallidae the belly and its origin are small and located on the anterior portion of the ventral surface of the distal fourth of the ulna (in _Aramus_ the muscle covers the whole distal half of the ulna). The small size seems to be correlated with the larger size of _M. flexor digitorum profundus_. In both rallids much more of the belly is covered by the latter muscle than in _Aramus_, and the connection to _M. anconeus_ is smaller. In neither _Rallus_ nor _Fulica_ is the tendon ossified or visible on the surface of the belly (ossified in _Aramus_ and conspicuous superficially).

Summary. The belly of this muscle is of a similar size in _Aramus_ and the cranes, but it is less than half as large in Rallidae. This relationship is the converse of that for _M. flexor digitorum profundus_, which is large in Rallidae and small in Aramidae and Gruidae. The sizes of the two muscles

are apparently correlated. _Aramus_ also agrees with the cranes in having the tendon visible superficially for most of the length of the belly, but the tendon forms only at the distal tip of the belly in the rallids. The insertion is essentially the same in all three families.

89. _M. abductor alae digiti_ II

Very small muscle composed of two entirely separate, flattened parts. Ventral (palmar) part somewhat elongate, dorsal (anconal) part ovate in dorsal view and slightly larger. Located on ventral and dorsal sides of base of extensor process of metacarpal II. Attaches to _M. extensor metacarpi radialis_, to extensor process of metacarpal II, and to phalanx (pollex) of digit II.

Lies partly deep to fascia associated with _M. tensor patagii longus_. Ventral part attaches to ventral side of distal end of tendon of _M. extensor metacarpi radialis_ and contacts anterior edge of _M. flexor digiti_ II. Dorsal part contacts posterior face of tendon of _M. extensor longus digiti_ II. Ventral part superficial to small portion of inserting tendon of _M. flexor carpi ulnaris brevis_.

Origin. Ventral part arises entirely from ventral edge of distal end of inserting tendon of _M. extensor metacarpi radialis_. Dorsal part arises mostly fleshily from area of junction of extensor process and dorsal (external) condyle of carpometacarpus, and partly from adjacent joint ligament.

Insertion. Ventral part inserts fleshily in trough along anteroventral face of proximal half of phalanx (pollex)

of digit II. Dorsal part forms narrow tendon, at distal end of belly, that inserts on dorsal edge of proximal end of same phalanx as ventral part.

Action. Extends alula.

Comparisons. The two bellies are fused distally (in Aramus they are entirely separate). In Balearica and G. canadensis (and Aramus) the ventral (palmar) belly arises entirely from the tendon of M. extensor metacarpi radialis with no origin from the overlying fascia of M. tensor patagii longus, but the origin is listed for G. americana as being from the tendon of the latter muscle and from the extensor process. In the three cranes the dorsal (anconal) belly arises from the extensor process (also partly from the dorsal trochlea in Aramus). In the cranes the insertions of the two bellies are partly fused (separate in Aramus), and the sites of attachment seem to correspond in all three cranes (and in Aramus).

In the Rallidae the ventral belly is fused to M. flexor digiti II, and the dorsal and ventral portions are fused distally (in Aramus there is no fusion to that muscle, and the two parts are entirely separate from each other). In both Rallus and Fulica the ventral belly arises from the tendon of M. extensor metacarpi radialis (as in Aramus), but also from the tendons of M. tensor patagii longus. The dorsal part arises mainly from the dorsal trochlea (in Aramus more origin is from the extensor process). In both rallids the dorsal belly inserts as in Aramus, but the ventral belly has,

in addition to the fleshy attachment, a small tendon extending to the distal tip of the digit (the latter is absent in _Aramus_). This more distal attachment and larger belly of the ventral part probably acts to produce more depression of the alula than in _Aramus_.

Summary. The limpkin resembles the cranes and differs from the rails in having the dorsal belly larger than the ventral and in having the insertion of the ventral part entirely fleshy and attaching on the proximal half of the phalanx. In the rallids the ventral belly is larger and has a tendon extending to the distal tip of the phalanx. Only in _Aramus_ are the two parts entirely separate from each other. The origin is slightly variable among the genera.

90. _M_. _adductor_ _alae_ _digiti_ II

Very small and flattened, triangular muscle. Located between phalanx (pollex) of digit II and metacarpal III. Attaches to metacarpal III, to phalanx of digit II, and to alular feathers.

In ventral view, proximal end deep to _M_. _abductor_ _major_ _digiti_ III. In dorsal view partly deep to _M_. _extensor_ _brevis_ _digiti_ II and to anterior branch of tendon of _M_. _extensor_ _digitorum_ _communis_.

Origin. Arises by fleshy and tendinous fibers from narrow facet about 6 mm long on anteroventral edge of metacarpal III, just distal to metacarpal II.

Insertion. Attaches fleshily and tendinously to posterior edge of phalanx of digit II and to ventral aspect of calami of alular feathers.

Action. Flexes (adducts) alula.

Comparisons. In the Gruidae the origin in *G. canadensis* is by a flat aponeurosis but is partly fleshy in the other two cranes (and *Aramus*). In *G. americana* the insertion is restricted to the distal end of the phalanx, but in the other two cranes (and *Aramus*) it inserts on most of the posterior edge. In *Balearica* only, *M. abductor major digiti* III arises from the edge of the origin. In *Balearica* (and *Aramus*) the muscle inserts partly on the alular feathers, but this attachment is not given for *Grus*.

In the Rallidae the condition of the muscle is very similar to that of *Aramus*, with the exception that in *Rallus* the insertion does not extend quite so far distad.

Summary. The muscle is in good agreement in all three families, with only insignificant variations among the genera.

91. *M. flexor digiti* IV

Very slender and elongate small muscle. Lies along posterior edge of manus. Attaches to metacarpal IV, to *M. flexor metacarpi posterior*, and to phalanx of digit IV.

In ventral view, muscle lies deep to strong fascial sheet. Proximal end adjoins distal end of *M. flexor metacarpi posterior*, and lies partly deep to it. Distal end lies posterior to distal end of *M. interosseus ventralis*.

Origin. Arises fleshily from posterior edge of distal three-fourths of metacarpal IV.

Insertion. Tendon forms within distal half of belly and continues distad to insert on phalanx of digit IV, on proximal face of small tubercle in middle of posterior edge of bone.

Action. Flexes wing tip.

Comparisons. In the Gruidae the belly in *Balearica* extends the full length of the metacarpal, but in *G. americana* it occupies only two-thirds of that bone (three-fourths in *Aramus*). In *G. canadensis* the belly is about half the length of the metacarpal. In *G. americana* there is a fascial attachment to primaries; this fascia is present in *Balearica* (and *Aramus*) but is not fused to the belly of the muscle.

In the Rallidae the belly in *Rallus* (and *Aramus*) arises from about three-fourths of the metacarpal, but in *Fulica* it originates from the full length.

Summary. The overall configuration of the muscle is similar in all three families, varying slightly among the genera, mainly in the extent of the belly.

92. *M. flexor brevis digiti* IV

This muscle appears to be represented entirely by a small group of connective tissue fibers in the posterior angle between the metacarpal and phalanx of digit IV.

Comparisons. In the Gruidae the structure in *Balearica* is similar to that of *Aramus*, but in *Grus* it apparently is somewhat larger with a few fleshy fibers.

In the Rallidae the muscle seems to be similar in size to that of *Aramus*, but appears to be composed entirely of fleshy fibers.

Summary. The muscle is fleshy in Rallidae, and mostly tendinous in Aramidae and Gruidae. The size is apparently larger in Grus than in Balearica and the non-gruids.

93. M. abductor minor digiti III

The material in this location, between the phalanx of digit IV and the first phalanx of digit III, is made up of loose connective tissue strands interspersed with a fat-like substance. No contractile bundles are recognizable under a dissecting microscope.

Comparisons. In the Gruidae Fisher and Goodman (1955) described a few contractile fibers in this area in G. americana and illustrated them (p. 44), but Berger (1956a) stated that he had never seen such a muscle, and that the structure in question is a tendon. This region in Balearica also lacks muscular fibers and resembles the same area in Aramus.

Summary. Although this may be a degenerate muscle, it acts entirely as a ligament in all genera studied here. Grus americana, the only species considered here that has contractile fibers, seems to be a partial exception.

94. M. flexor metacarpi brevis

Minute muscle composed of slender, cylindrical belly giving rise to very small, rounded tendon at either end. Lies on dorsal side of proximal end of metacarpal III. Connects to radiale bone and to M. extensor longus digiti III.

Hudson and Lanzillotti (1955) consider this muscle to be a distal head of M. extensor longus digiti III.

Partly deep to both branches of inserting tendon of _M_. _extensor digitorum communis_. Anterior to tendon of _M_. _extensor longus digiti_ III, with distal end connected to it.

Origin. Arises by very slender tendon from dorsal side of radiale.

Insertion. Tendon, similar to one of origin, fuses with tendon of _M_. _extensor longus digiti_ III about one-third of way distad on metacarpal II.

Action. Fisher (1946) lists this as a flexor in the cathartids, but in _Aramus_ it seems to extend digit III, as well as the whole hand.

Comparisons. In the Gruidae the belly in _Balearica_ is slightly larger and flatter than in _Aramus_. The muscle is lacking in both species of _Grus_.

In the Rallidae the muscle is absent.

Summary. The muscle is similarly well developed in _Aramus_ and _Balearica_, but it is not present at all in _Grus_ or the two rallids. The intrafamilial variation in the Gruidae corroborates Berger's idea (1956a) that the muscle may be of taxonomic value in some families. Its apparent function in _Aramus_ is as an extensor, although Fisher describes it as a flexor in cathartidae.

95. _M_. _interosseus dorsalis_

Elongate and rather small muscle with bipinnate belly, continued distally as long, slender tendon. Lies in dorsal portion of intermetacarpal space. Attaches to metacarpals III and IV and to phalanx 2 of digit III.

Proximal end of belly contacts insertion of *M. flexor metacarpi radialis*. Deep side of belly contacts *M. interosseus ventralis*.

Origin. Arises mostly fleshily from posterodorsal edge of metacarpal III and from anterodorsal edge of metacarpal IV. Origin extends from proximal end almost to distal end of intermetacarpal space.

Insertion. Small, flattened tendon continues from distal end of belly, passes down dorsal side of phalanx 1 of digit III, and inserts strongly on anterodorsal edge of proximal end of phalanx 2. Insertion lies posterodorsal to distal insertion of *M. extensor longus digiti* III.

Action. Elevates digit III and attached primaries.

Comparisons. In the Gruidae the belly in *Balearica* (and *Aramus*) extends as far as the distal end of the intermetacarpal space, but in *Grus* it is restricted to the proximal two-thirds of that space. Apparently only in *G. canadensis*, a small tendon extends distad from the main insertion.

In the Rallidae the muscle is unevenly bipinnate (symmetrical in dorsal view in *Aramus*), but otherwise very similar to that of *Aramus*.

Summary. Variations in this muscle are restricted mainly to slight differences in the size and shape of the belly among the genera of the three families.

96. *M. interosseus ventralis*

Elongate, somewhat flattened muscle with bipinnate belly, continued distally as long and slender tendon. Located in

ventral portion of intermetacarpal space. Attaches to metacarpals III and IV and to phalanx 2 of digit III.

Proximal end contacts _M_. _flexor_ _metacarpi_ _posterior_ and _M_. _abductor_ _major_ _digiti_ III. Deep side of belly contacts _M_. _interosseus_ _dorsalis_.

Origin. Originates mostly fleshily from entire length of posteroventral edge of metacarpal III and from full length of anteroventral edge of metacarpal IV.

Insertion. Belly passes onto dorsal side of carpometacarpus and gives rise to small tendon at distal end; tendon continues distad along posterodorsal edge of phalanx 1 of digit III and inserts strongly on posterodorsal edge near distal end of phalanx 2.

Action. Elevates and flexes digit III.

Comparisons. In the Gruidae the insertion in _Balearica_ (and _Aramus_) is very near the distal end of phalanx 2, but in _Grus_ the muscle attaches three-fourths of the way out the phalanx. In _G_. _canadensis_ it has an additional attachment to the base of the phalanx.

In the Rallidae the belly in _Rallus_ is smaller than in _Aramus_, but in _Fulica_ the belly is larger than in _Aramus_. Otherwise the muscle in both rallids is like that of _Aramus_.

Summary. The pattern is quite uniform among the genera. Differences occur only in the point of insertion in Gruidae and in the size of the belly in Rallidae, but these are very minor.

97. _M._ _extensor_ _brevis_ _digiti_ II

Very small, elongately triangular muscle with short, narrow tendon leading from distal end of belly. Located on dorsal side of phalanx (pollex) of metacarpal II and on portions of metacarpal III immediately posterior to base of phalanx. Attaches to metacarpal III and to claw of phalanx of digit II.

Lies just posterior and distal to _M._ _abductor_ _alae_ _digiti_ II and anterior to _M._ _adductor_ _alae_ _digiti_ II. Superficial and connected to distal end of anterior branch of inserting tendon of _M._ _extensor_ _digitorum_ _communis_.

Origin. Arises fleshily from small, oval area on anterodorsal face of proximal region of metacarpal III, just posterior to base of phalanx of digit II.

Insertion. Slender tendon forms at distal end of belly, passes along posterior edge of dorsal face of phalanx of digit II, and inserts on dorsal edge of base of claw.

Action. Elevates digit II and extends claw.

Comparisons. In the Gruidae the insertion in _Balearica_, but not in _Grus_ (or _Aramus_), has small, tendinous branches to the calami of the alular feathers. In _Balearica_, (as in _Aramus_) there is also insertion on the distal claw. Other features are similar in all three cranes (and _Aramus_).

In the Rallidae the muscle inserts on the alular feathers and fleshily onto the distal half of the phalanx, without forming a definite tendon (in _Aramus_ the insertion is by a well defined tendon, onto the distal end of the phalanx and the claw).

Summary. *Balearica* agrees with the Rallidae in having some of the insertion on the alular feathers, but this attachment is absent in *Aramus* and *Grus*. Apparently only in *Aramus* and *Balearica* is there insertion on the distal claw. *Aramus* agrees with Gruidae in having a definite tendon, but the insertion is mostly fleshy in Rallidae.

98. *M. abductor major digiti* III

Small muscle composed of attenuate, bipinnate belly that extends to distal end of intermetacarpal space and short, distal tendon. Belly partially separated into superficial and deep portions. Located on anteroventral edge of metacarpal III. Attaches to metacarpal III and to phalanx 1 of digit III.

Proximal end of belly partly deep to belly of *M. flexor digiti* II and contacts bellies of *M. interosseus ventralis* and *M. adductor alae digiti* II. Full length of ventral side of belly partly deep to tendons of *M. flexor digitorum profundus* and *M. flexor digitorum sublimus*.

Origin. Arises fleshily from elongate area on most anteroventral edge of metacarpal III. Proximal end of this area wider, extending from base of extensor process, across distal face of pisiform process, to area of fusion of metacarpals III and IV. Deep portion of belly lies distal to extensor process.

Insertion. Superficial and deep portions fuse completely in middle of belly, and ossified tendon forms superficially along distal two-thirds of belly. Tendon loses

ossification at distal end of metacarpal, becomes flattened, and inserts strongly into notch on anterior edge of proximal end of phalanx 1 of digit III.

Action. Extends, and perhaps depresses, digit III.

Comparisons. In the Gruidae the origin in *Balearica*, but not in *Grus* (or *Aramus*), is partly from *M. adductor alae digiti* II. In *Balearica* fleshy fibers extend to distal end of metacarpal III (in *Aramus* the belly extends to the distal end of the intermetacarpal space), but in *Grus* the fleshy fibers end in the middle of the length of the metacarpal. The tendon is strongly ossified in *Balearica* and *G. canadensis* (and *Aramus*), unknown for *G. americana*.

In the Rallidae the separation into superficial and deep portions is lacking in *Rallus* but is present in *Fulica* (and *Aramus*). In neither rallid is the tendon ossified (strongly ossified in *Aramus*). In both *Rallus* and *Fulica* fleshy fibers extend to the distal end of metacarpal III (extend only to distal end of intermetacarpal space in *Aramus*).

Summary. The comparative differences in this muscle are minor. Only *Rallus* lacks the partial division of the belly, and only in *Grus* does the belly not extend almost to the distal end of metacarpal III. The rallids, and perhaps *G. americana*, lack ossification of the tendon, but in *Aramus* and the other two gruids the tendon is strongly ossified.

99. *M. flexor digiti* II

Very small muscle with short, narrow belly and short distal tendon. Located on ventral face of proximal end of

carpometacarpus and on phalanx of digit II. Attaches to joint ligament, to carpometacarpus, and to phalanx and claw of digit II.

Belly contacts posterior edge of belly of ventral part of _M. abductor alae digiti_ II and contacts proximal end of _M. abductor major digiti_ III. Superficial to tendons of _M. flexor digitorum profundus_ and _M. flexor digitorum sublimus_.

Origin. Originates mainly fleshily, but also by small tendinous components, from anteroventral corner of ventral (internal) trochlea of carpometacarpus, from ventral face of base of extensor process, tendinously from anterodistal edge of pisiform process, and fleshily from joint ligament connecting radius with pisiform process.

Insertion. Attaches fleshily to ventral face of base of phalanx of digit II and also by small tendon attaching to ventral edge of distal third of phalanx and to claw at distal end.

Action. Pulls alula ventrad and posteriad and flexes claw.

Comparisons. In the Gruidae a small portion originates from the pisiform process in _Balearica_ (and _Aramus_, but this is absent in _Grus_. The origin from the joint ligament is absent in all three cranes (present in _Aramus_), as is the small tendon continuing from the main insertion to insert on the distal end of the phalanx and on the claw of digit II (present in _Aramus_).

In the Rallidae the belly of this muscle is intimately fused with the ventral belly of _M. abductor alae digiti_ II,

but its extent seems to be similar to that in Aramus; the small distal tendon (of Aramus) is lacking.

Summary. Aramus agrees with Gruidae and differs from Rallidae in having the muscle distinctly separate from M. abductor alae digiti II. The origin is somewhat variable in the three families, and only in Aramus is there a small tendon extending to the claw.

100. M. flexor metacarpi posterior

Small but thick, triangular mass of muscle, composed of three partially separate bellies. Posterior belly bipinnate and larger, enfolding other two portions both dorsally and ventrally. Intermediate portion smaller and more compact but partially enfolds anterior portion, which is smallest. Located in angle between forearm and hand. Attaches to ulna, to carpometacarpus, and to fascia associated with primary feathers.

Distal end adjoins proximal end of M. flexor digiti IV. Tendons of M. flexor metacarpi radialis and M. extensor digitorum communis run along anterior edge of belly.

Origin. All three bellies originate in common by narrow aponeurosis from semilunar line on dorsal surface of extreme distal end of shaft of ulna. All three parts arise as fleshy continuations of this tendon. Aponeurosis of origin continuous with fascia over dorsal side of wrist.

Insertion. Posterior portion inserts fleshily onto ligamentous bands connected to calami of primaries on dorsal side of hand and onto fascia covering M. flexor digiti IV on

ventral side. Intermediate portion attaches fleshily to most of proximal third of posterior face of metacarpal IV. Anterior portion inserts on same bone, on triangular area set into proximal edge of previous insertion and bordered proximally by trochleae.

Action. Main action flexes hand, but superficial portion apparently also helps expand primaries.

Comparisons. In the Gruidae the posterior belly apparently includes the dorsal half of the same portion in *Aramus* and therefore covers only the dorsal side of the other two bellies (completely encloses the other two in *Aramus*). In none of the cranes does this belly have bipinnate structure like that of *Aramus*, but in *Balearica* a different bipinnate organization is present, apparently as a result of fusion with the anterior part. The intermediate belly is fleshy and similar in *Balearica* and *G. americana* (and in *Aramus*), but in *G. canadensis* it is mostly tendinous. In *Balearica* the portion corresponding to the anterior belly is fused with the anterior edge of the superficial portion, but in *Grus* it is tendinous and separate (fleshy and separate in *Aramus*). In *Balearica* (and *Aramus*) the posterior belly inserts on ligamentous attachments of primaries, but in *Grus* it inserts on metacarpal IV.

In the Rallidae the posterior belly is not as large as in *Aramus*. The insertion of the posterior belly in *Rallus* is on metacarpal IV as well as on the primaries, but in *Fulica* (and *Aramus*) this insertion is only on the latter. In *Rallus*

(and _Aramus_) the muscle has three bellies, but in _Fulica_ the small, anterior belly is either absent or fused with one of the other two.

Summary. The size and extent of the posterior belly is different for each family. In _Balearica_, and apparently also in _Fulica_, two of the bellies are fused. In _Aramus_, _Balearica_, and _Fulica_ the insertion of the posterior belly is entirely on the ligaments of the primaries, but in _Grus_ it attaches only to the metacarpal. In _Rallus_ both the previous attachments are represented. In _Grus_ more of the muscle is tendinous than in _Balearica_ or the non-gruids.

Muscles of the Tail

101. _Mm. adductor rectricum_

Series of five very short and very small dermal muscles and one small but rather elongate one. Series of five lies between bases of rectrices, just inside posterolateral edge of fleshy portion of tail. Elongate muscle lies on ventral side and runs transversely across inner five rectrices, just anterior to five short mus cles. All muscles are usually embedded in fat. These muscles connect to all six rectrices on either side.

Complex lies completely posterior to other components of caudal musculatire.

Origin and Insertion. Each small muscle arises from lateral side of one medial rectrix and inserts on medial side of next one lateral to it. Elongate, ventral muscle arises

from ventral surface of most medial rectrix and inserts on ventral surface of each of others except the most lateral.

Action. Combined action of complex adducts all rectrices except inner one, which is anchored to pygostyle.

Comparisons. In the Gruidae the five small muscles between the rectrices in *Balearica* are continuous on the dorsal side by a narrow, partly muscular sheet that has a series of pointed anterior projections, one at each rectrix, connecting to the superficial fascia over the fleshy portion of the tail but not attaching to the pygostyle. Ventrally, a slightly wider but similar sheet is present, connecting each of the small muscles and attaching to the pygostyle (this ventral sheet seems to correspond to the elongate ventral belly in *Aramus*). In *Grus* the small muscles between the first and third rectrices are connected (all these are separate in *Aramus*). In *Grus*, as in *Balearica*, there is a muscle arising from the pygostyle and inserting on the most medial rectrix (this connection seems to lack contractile fibers in *Aramus*).

In the Rallidae the connections in *Rallus* between the rectrices are separate and arranged in a manner similar to that of *Aramus*, but they are very small and appear to be composed entirely of connective tissue (fleshy in *Aramus*). Nothing is found to correspond to the elongate ventral slip of *Aramus*. In *Fulica* the small muscles are larger and appear fleshy, with a narrow sheet joining all of them on the ventral side (this sheet seems equivalent to the elongate ventral belly of *Aramus*).

Summary. This muscle complex is different in each genus. In *Aramus* and *Rallus* the small muscles are entirely separate, but in *Rallus* they are reduced to ligamentous structures. In *Grus* there is some dorsal connection between the most medial two muscles, but in *Balearica* all the muscles are continuous both dorsally and ventrally. In *Fulica* they are continuous only ventrally. Only in *Aramus* is there a separate transverse belly on the ventral side.

102. *M. levator coccygis*

Rather small but bulky muscle, approximately triangular in dorsal view. Posterior half divided into five small fasciculi that run posteromediad. This muscle forms most anterior and dorsal portion of caudal musculature. Attaches to sacrum, to last fused and to first four free caudal vertebrae, and to dorsal *Mm. interspinales* of tail.

Posterior half of muscle covered by uropygial gland, and whole muscle enclosed by fascial sheet. Lies superficial to all but posterolateral third of *M. levator caudae* and has slight connection to it.

Origin. Arises almost entirely fleshily from dorsal face of sacrum, from lachrymiform area involving posterior extent of vertebral region. Adjoins inner portion of ilium, and extends anteriorly to level of antitrochanters.

Insertion. Each of five small fasciculi gives rise to small aponeurosis that inserts along with an inner, fleshy portion onto lateral face of neural spine of one caudal vertebra. The most anterior and medial slip inserts on last

fused vertebra. Each successively more posterior and more lateral slip attaches to successive free vertebrae, one through four. Insertions connect to Mm. interspinales.

Action. Combined action of all attachments on one side pulls tail laterad, and both sides acting together raise tail. Insertion of first slip apparently non-functional, being on a fused vertebra.

Comparisons. In the Gruidae the muscle in Balearica, and sometimes in Grus, has four fasciculi, but in Grus the usual number is three (five in Aramus). In Balearica the underside of the belly is closely fused to M. levator caudae (in Aramus there is only a slight connection), but the two muscles are not fused in Grus. In Balearica (and Aramus) the origin is almost entirely fleshy, but in Grus the anterior half is aponeurotic. In Grus alone, the muscle arises partly from the first free caudal vertebra, but this may be equivalent to one of the fused caudals in Balearica (and Aramus). In Balearica the most anterior fasciculus inserts on the last fused and the first and second free caudals, but in Grus it inserts on the third free caudal (on the last fused vertebra in Aramus). In Balearica the second slip attaches mainly to the second free caudal and indirectly to the third, but in Grus this insertion is on the fourth (on the first free caudal in Aramus). In Balearica the third slip inserts on the fourth free caudal and on the fifth in Grus (on the second in Aramus). In Balearica the fourth fasciculus inserts on the fourth and fifth free caudals, and in Grus, when present, on

the pygostyle (on the third free caudal in _Aramus_). Neither _Balearica_ nor _Grus_ has a fifth fasciculus (present in _Aramus_). A skeleton of _Balearica_ indicates that ossified tendons may arise within the belly of this muscle and attach to the last fused vertebra. In both cranes (and _Aramus_) the muscle is enclosed in a similar fascial sheet.

On the Rallidae the muscle is more elongate than in _Aramus_. Five fasciculi are present in _Rallus_ (and _Aramus_) and six in _Fulica_. Because of the more elongate sacrum the origin in both rallids is located considerably posterior to that of _Aramus_, and the narrower sacrum allows the belly to touch _M. flexor cruris lateralis_ (in _Aramus_ there is no contact with that muscle). In _Rallus_ each of the five fasciculi inserts on the free caudal of the corresponding number. In _Fulica_ each of the six slips inserts on the corresponding free caudal, but the first three slips are barely separable from each other (in _Aramus_ the first slip inserts on the last fused caudal, and slips two through five insert on free caudals one through four, respectively). In both rallids the fasciculi nearer the anterior end are mostly fleshy (mostly tendinous in _Aramus_). In both rallids (as in _Aramus_) the muscle is completely enclosed in fascia.

Summary. Although the general pattern of the muscle is recognizably similar in each of the five genera, there appears to have occurred fusion, and perhaps splitting, of some fasciculi. The points of insertion seem to vary considerably, but because of differences in the numbers of vertebrae fused

to the sacrum, it is difficult to establish corresponding vertebrae in the various genera. The muscle is more elongate in Rallidae than in _Aramus_ and Gruidae, but this seems merely to be a reflection of the elongated sacrum of the rallids. The smallest number of fasciculi occurs in Gruidae and the greatest number in _Fulica_; _Aramus_ and _Rallus_ are intermediate.

103. _Mm. interspinales_

Series of small, largely elastic muscles divided into dorsal and ventral sets. Some of dorsals in cervical ragion fused to form long elastic fasciculus. Dorsals in cervical region unpaired, but paired in caudal region; ventral set unpaired. Dorsals located between vertebrae along dorsal midline of neck, body, and tail, and are absent only between atlas and axis and on pelvis. Ventrals located only on caudal vertebrae. Whole series attaches to nearly all vertebrae. to connective tissue below pelvis, and to _M. levator coccygis_.

In cervical region dorsals lie deep to _M. spinalis cervicis_ and _Mm. intercristales_. In caudal region dorsals bounded laterally by _M. levator coccygis_, and ventrals deep to _M. lateralis coccygis_ and bordered laterally by _Mm. intercoccyges_.

Origin. In cervical region dorsals arise from small scar near base of anterior edge of neural spine. Long fasciculus arises mainly from neural spine of fifteenth vertebra. In caudal region dorsals arise from posterolateral corner of dorsal extent of neural spines of free caudal vertebrae and

from adjacent region of pelvis, and ventrals arise from posteroventral corners of hypapophyses of caudal vertebrae.

Insertion. In cervical region most of dorsals insert on small scar near base of posterior edge of neural spine of cervical vertebrae. Long fasciculus attaches to dorsal face as well as to portions of both anterior and posterior faces of neural spines of fourteenth through eleventh cervicals. In caudal region each dorsal inserts on anterolateral corner of dorsal extent of neural spine of one caudal vertebra. Ventrals insert on anteroventral corners of hypapophyses of caudal vertebrae.

Action. Judging from sparseness of fleshy tissue, tendinous muscles of the series apparently act as elastic tendons that help maintain normal posture and help to automatically return vertebrae to normal resting positions.

Comparisons. In the Gruidae *Balearica* (and *Aramus*) lacks the series between the first two vertebrae but it is present throughout the remainder of the neck and thorax. In *Grus* the series is present between the first two vertebrae but is absent between the sixth and seventeenth vertebrae. In *Balearica* the fasciculi between the twelfth and sixteenth are fused into one long fasciculus (fused between the eleventh and fifteenth in *Aramus*). In *Grus* the fasciculi in this region are apparently separate.

In the Rallidae (as in *Aramus*) dorsals are small but are present throughout the neck and thorax except between the first two cervicals. In both rallids the slips are entirely simple

(in <u>Aramus</u> some are united into one long fasciculus). In both rallids the dorsals of the caudal region show some evidence of a paired condition, but the parts are closely connected in the mid-line (in <u>Aramus</u> these muscles are more distinctly paired). In both rallids the ventrals are narrower than in <u>Aramus</u>.

<u>Summary</u>. In <u>Grus</u> only, the dorsals are present between the first two vertebrae and absent in the middle of the neck. In the rallids the dorsals are smaller than in the other two families. In <u>Aramus</u> and <u>Balearica</u>, but not in <u>Grus</u> or the Rallidae, some fasciculi in the posterior cervical region are fused into one long fasciculus. In <u>Aramus</u> and the Gruidae the caudal dorsals are distinctly paired, but in the Rallidae the separation is indistinct. In both rails the ventrals are narrower than in the non-gruids.

104. <u>M</u>. <u>levator</u> <u>caudae</u>

Small and elongate muscle. Dorsal half divided into three small fasciculi, and ventral half horizontally flattened. Lies just lateral to mid-line, alongside caudal vertebrae. Attaches to ilium, to caudal vertebrae, to pygostyle, to <u>M</u>. <u>levator</u> <u>coccygis</u>, and to fleshy base of attachment of rectrices and major upper coverts.

All but anterolateral third deep to, and slightly connected to, <u>M</u>. <u>levator</u> <u>coccygis</u>, and remainder lies ventral to uropygial gland. Superficial to anteromedial portion of <u>M</u>. <u>lateralis</u> <u>caudae</u> and to posterior end of <u>M</u>. <u>lateralis</u> <u>coccygis</u>.

Origin. Arises fleshily from extreme posteromedial end of ilium and from entire dorsal surface of caudal vertebra and first three free caudals, as well as from fascia connecting those processes.

Insertion. Dorsal half of belly divides into three slips. Most anteromedial one inserts fleshily on side of neural spine of fourth free caudal. Next fasciculus attaches by small tendon to dorsal tips of neural spines of fifth and sixth free caudals. Most posterolateral fasciculus inserts by small tendon on anterolateral edge of pygostyle. Ventral half of belly becomes separate fasciculus that passes from beneath previous slip and widens to fuse with fleshy portion of tail, into which rectrices and major upper coverts are embedded. Small group of bundles also leaves posterolateral corner of fleshy portion of tail and inserts on uropygial gland.

Action. One muscle pulls tail laterad, but muscles on both sides acting together elevate tail and major upper coverts.

Comparisons. In the Gruidae the muscle in _Balearica_ is divided into one dorsal and one wide, ventral fasciculus. In _Grus_ (and in _Aramus_) it is divided into three dorsal slips and one ventral fasciculus. In _Balearica_, but not in _Grus_, the muscle is closely fused to _M. levator coccygis_ (slightly fused in _Aramus_). In both cranes (and _Aramus_) the muscle arises partly from the ilium. In _Balearica_ it also arises from the sides of the first three free caudals and from the

transverse processes of the last fused and first two free caudals. In Grus (and Aramus) the origin from the sides of the vertebrae is lacking, but in Grus the muscle arises from the same transverse processes and also from the transverse processes of the next to the last fused, and from the third free caudal. In Balearica the dorsal fasciculus inserts only on the pygostyle, but in Grus the three dorsal fasciculi attach to the fourth and fifth free caudals as well (in Aramus they insert on the fourth, fifth, and sixth free caudals, as well as on the pygostyle). The insertion of the ventral slip is rather constant, but in Balearica (and Aramus) it seems to connect to only three or four rectrices, whereas it attaches to five in Grus. In both cranes (and Aramus) there is some insertion on the oil gland.

In the Rallidae a single dorsal fasciculus is present (three are present in Aramus), and it inserts on the seventh free caudal as well as on the pygostyle. This double attachment is accomplished by two tendons in Rallus and by one branched tendon in Fulica. In both rallids the ventral portion is small and inserts only on the most medial rectrices (wider in Aramus), but a small portion inserts on the oil gland in both (as well as in Aramus).

Summary. This muscle is rather thick in the cranes and Aramus but very narrow in Rallidae. There are three dorsal fasciculi in Aramus and Grus, but only one in Balearica and Rallidae. The origin is most extensive in Balearica, and the insertion most extensive in Aramus and Grus. The insertion

of the ventral portion is widest in _Grus_, intermediate in _Aramus_ and _Balearica_, and narrowest in Rallidae.

105. _M. lateralis caudae_

Small, irregularly shaped muscle with two parts, slightly elongate anterolateral part and somewhat sheet-like posteromedial part. Makes up most lateral portion of caudal musculature. Attaches to ilium, to strong aponeusosis at posterior edge of ilium, to caudal vertebrae, to pygostyle, to bases of rectrices, to upper coverts, and to _M. lateralis coccygis_.

Posterior and medial portions partly deep to _M. levator coccygis_ and to _M. levator caudae_. Superficial to _M. lateralis coccygis_.

Origin. Anterolateral part originates, mostly tendinously, from posterior edge of ilium, from strong fascial sheet at posterior edge of ilium, and from lateral edges of last fused and first free caudal vertebrae. Posteromedial part arises, mostly tendinously, from lateral edges of first three free caudals.

Insertion. Anterolateral part passes posteriad to insert fleshily on dorsal and medial sides of most lateral rectrix. Posteromedial part fuses with posteromedial slip of _M. lateralis coccygis_ and common muscle inserts as sheet on dorsal surface of all six rectrices, and on bases of upper coverts, and continues posteromedially to insert on ventral region of anterior edge of pygostyle.

Action. Pulls tail dorsolaterad, but both muscles acting together raise tail and spread rectrices.

Comparisons. In the Gruidae the posteromedial part differs from that of Aramus in being very thick and in not forming a common sheet with M. lateralis coccygis. In Balearica the origin does not extend anteriorly quite as far as the ilium, but in Grus the posteromedial part arises partly from that bone(and in Aramus the anterolateral part arises partly from the ilium). In Balearica (and Aramus) the anterolateral part arises from the last fused and the first free caudal, but in Grus it does not originate from the vertebrae. In Balearica the posteromedial part arises partly from each free caudal (from only the first three in Aramus). In Grus it arises from the last fused and first three free caudals. The extent of the insertion of both parts is similar in the two gruids (and in Aramus, except that the muscle connects to M. lateralis coccygis).

In the Rallidae the muscle is similar to that of Aramus, differing mainly in not arising from the ilium and in not fusing so strongly with M. lateralis coccygis. In Fulica there is no origin from the ilium, and the posteromedial part inserts partly on the uropygial gland, apparently because of the more deepseated location of the gland, and there is very little attachment to the rectrices. In Rallus (and Aramus) there is no insertion on the gland, but the attachment to the rectrices is larger.

Summary. The anterolateral part is rather similar in all three families, but it arises from the ilium only in Aramus and Grus. The posteromedial part is thick in Gruidae,

but is sheet-like in Aramus and Rallus. It is greatly shortened in Fulica because of the deepseated condition of the oil gland, but a similar condition of the gland in Rallus has not affected the muscle. In Aramus the posteromedial part fuses with M. lateralis coccygis, but in Rallus this connection is weak, and it is absent in Fulica and the cranes.

106. M. depressor caudae

Small and flattened, triangular muscle. Located in ventrolateral portion of caudal musculature. Attaches to pubis and to medial rectrices and coverts.

Ventral end deep to M. transverso-analis and to M. flexor cruris lateralis. Superficial to portions of M. lateralis caudae, M. levator cloacae, and to M. depressor coccygis.

Origin. Arises fleshily and tendinously from dorsal edge of portion of pubis posterior to ilium.

Insertion. Inserts fleshily on ventrolateral portion of calamus of most lateral rectrix, partly in common with insertion of anterolateral part of M. lateralis caudae.

Action. One muscle depresses one side of tail, but muscles of both sides act together to depress whole tail.

Comparisons. In the Gruidae the muscle is larger and wider than in the limpkin. In both gruids it originates from the ilium, ischium, ischio-public ligament, and the interpublic ligament, in addition to its origin from the pubis (in Aramus it arises only from the pubis). The insertion is approximately the same in both cranes (and Aramus).

In the Rallidae the muscle is distinctly different from the muscle in Aramus in being composed of two parts. The origin of the larger part in the rallids is extensive, arising from the entire posterior end of the pubis and from the body wall between the pubis and M. sphincter ani. The smaller, superficial part inserts on the ventrolateral edge of the fleshy portion of the tail (corresponds to the single insertion in Aramus). In the two rallids the larger, deep part inserts separately, just posteromedial to the previous attachment (in Aramus only one part, with one insertion, is present).

Summary. The muscle in Aramus and the cranes is distinctly different in some points from that of the Rallidae but shows a good gruid-rallid similarity in others. In the rallid the muscle has two parts, but in Aramus and Gruidae there is only one part. The size of the muscle agrees well in Gruidae and Rallidae, being more than twice as wise as in Aramus. In Aramus the origin is only from the pubis, in the gruids it arises from the ischium and ilium as well as from the pubis, but in the rallids it arises from the body well. In the rails the two parts insert separately, but in Aramus and the cranes there is only one insertion.

107. M. levator cloacae

Very slender and elongate muscle, 1 mm wide. Located between lateral surface of tail and cloaca. Connects to most lateral rectrix and to cloaca wall.

Most of belly deep to M. depressor caudae but extreme ventral end deep to M. sphincter ani. Superficial to portion of M. depressor coccygis.

Origin. Arises from ventral surface of tip of calamus of most lateral rectrix.

Insertion. Attaches fleshily to dorsolateral wall of cloaca.

Action. Raises cloaca.

Comparisons. In the Gruidae the origin in _Balearica_ (and _Aramus_) is from the most lateral, or sixth, rectrix, but in _Grus_ it is from the fourth. The insertion is constant in both cranes (and in the limpkin).

In the Rallidae the muscle is somewhat wider than in _Aramus_, especially at the ventral end in _Rallus_. The origin in _Rallus_ is from the region between the fifth and sixth rectrices, and from the most lateral, or seventh, rectrix in _Fulica_ (in _Aramus_ it arises fxm the most lateral, or sixth, rectrix). The location of the insertion is similar in both rallids (and _Aramus_).

Summary. The muscle is more slender in _Aramus_ and the gruids than in the rallids. The location of the origin is associated with the most lateral rectrix in _Aramus_, _Balearica_, and _Fulica_, but is located more medially in _Grus_ and _Rallus_.

108. _M. depressor coccygis_

Somewhat triangular in lateral view; wide and sheet-like in ventral extent, narrower and thicker at dorsal end. One of deep muscles of ventrolateral portion of caudal musculature. Attaches to ischium, to pubis, to ischio-pubic ligament, and to ventromedial area of fleshy portion of tail.

Partly deep to _M_. _depressor_ _caudae_ and to _M_. _levator_ _cloaca_.

Origin. Arises by aponeurosis from dorsal edge of posterior portion of pubis, deep to origin of _M_. _depressor_ _caudae_. Arises also, mostly fleshily, from posterior edge of ischium and from ischio-pubic ligament.

Insertion. Attaches fleshily and tendinously on small area of ventral fascia associated with insertion of _M_. _lateralis_ _coccygis_ on fleshy portion of tail. Insertion located just lateral to mid-line and contacts insertion of corresponding muscle on other side.

Action. Depresses tail.

Comparisons. In the Gruidae the muscle in _Balearica_ (and _Aramus_) has a slightly less extensive origin than in _Grus_. In _Balearica_ the insertion is on the medial three rectrices, but on the medial four in _Grus_ (narrower in _Aramus_, associated with only the medial two rectrices). In both cranes (and _Aramus_) the muscle contacts the one from the other side across the mid-ventral line.

In the Rallidae the muscle is slightly smaller than in _Aramus_, but in _Fulica_ it is considerably more extensive than in _Aramus_. In both rallids the origin is located farther posterior than in _Aramus_. In _Rallus_ it arises from the posterior extent of the pubis and from a small area of fascia on the body wall at the posterior end of the pubis, but in _Fulica_ the muscle arises from the same area of the pubis but also from the fascia of the body wall, all the way to the lateral

wall of the cloaca (in _Aramus_ it arises from the ischium and the pubis). In _Rallus_ (as in _Aramus_) the insertion is small and near the mid-line, but in _Fulica_ it is wider and extends farther laterally.

Summary. This muscle is relatively narrow in _Aramus_ and _Rallus_, wide in the Gruidae, and very wide in _Fulica_. The origin is farthest anterior in the non-rallids, mors posterior in _Rallus_, and extends farthest posteriorly in _Fulica_. The insertion in _Fulica_ is somewhat wider than in the other four genera.

109. _M. lateralis coccygis_

Bulky muscle composed of three fasciculi. Two most ventral fasciculi run full length of muscle, partly connected to each other. Posteromedial fasciculus short and partly encloses tips of calami of rectrices. Makes up bulk of ventrolateral portion of caudal musculature. Attaches to last fused caudal vertebrae, to free caudals, to _M. lateralis caudae_, to rectrices, to ventral coverts, and to _M. depressor coccygis_.

Lies deep to _M. lateralis caudae_ and to _M. levator caudae_.

Origin. Two ventral fasciculi arise from ventral faces of transverse processes of last two fused caudals and first two free caudals. Posteroventral fasciculus arises from transverse processes of last four free caudals.

Insertion. Most ventral fasciculus widens, becomes aponeurotic at posterior end, and attaches to ventral surface of fleshy tissue holding ventral coverts. Long fasciculus

lying just dorsal to latter inserts fleshily around bases of ventral coverts and on ventral side of calami of rectrices. Posteromedial slip inserts partly on ventral edge of pygostyle, partly by aponeurosis to most medial rectrices, and partly by fleshy slip that fuses with posteromedial part of *M. lateralis caudae*. This slip encloses tips of rectrices and *M. expansor rectricum*, and inserts on dorsal side of calami of rectrices.

Action. Depresses tail and spreads rectrices, but muscle on one side may also slightly abduct tail.

Comparisons. In the Gruidae the main belly of this muscle is not divided (composed of three mostly separate fasciculi in *Aramus*). The origin in the two cranes, from the ilium and fused caudals, appears similar (but in *Aramus* the origin from the ilium is lacking). The extent of the main insertion is similar in both *Balearica* and *Grus* (and corresponds to the insertion of the two ventral fasciculi in *Aramus*). The attachments to the pygostyle are similar in both cranes (but in *Aramus* they are from the common sheet formed by the posteromedial fasciculus and *M. lateralis caudae*. In *Balearica* a portion of the muscle passes dorsad around the anterior tips of the rectrices and beneath the portion of *M. lateralis caudae* in this area. This portion is apparently absent in *Grus* (in *Aramus* it is in common with *M. lateralis caudae*).

In the Rallidae this muscle is rather similar to that of *Aramus*. The two long ventral fasciculi are similar to those

of Aramus. The posteromedial slip does not fuse with M. lateralis caudae (fuses with that muscle in Aramus), but it does not attach to the rectrices(as in Aramus).

Summary. The extent and size of this muscle is constant in all three families, but in Aramus and Rallidae it divides into three fasciculi. The only divisions in Gruidae are small fasciculi attaching to the pygostyle. In Aramus the posteromedial slip fuses with M. lateralis caudae and encloses the anterior tips of the rectrices. There is no such fusion in Gruidae or Rallidae, but the same insertion is present in both families, with the apparent exception of Grus.

110. Mm. intercoccyges

Series of extremely small and flat, paired, triangular muscles, which appear rudimentary and mostly fascial. Located just lateral to mid-line, between successive caudal vertebrae. Attach to caudal vertebrae, including pygostyle.

Completely enclosed, dorsally by M. lateralis caudae and ventrally by M. lateralis coccygis. Lie just lateral to ventral Mm. interspinales.

Origin. Each muscle arises from width of transverse process of one caudal vertebra.

Insertion. Each muscle passes posteriad to insert on hypapophysis of caudal vertebra just posterior to one from which it arose.

Action. Combined action on one side bends tail laterad.

Comparisons. In the Gruidae these muscles are greatly reduced, even more than in Aramus, and Fisher and Goodman (1955) reported them absent in Grus.

In the Rallidae the muscles are larger, rather obvious, and entirely fleshy in both rallids.

Summary. The muscles are apparently rudimentary in Aramus, even more reduced in Balearica, and completely absent in Grus. In Rallidae they are well developed and typical of birds (see Shufeldt, 1890).

111. M. expansor rectricum

Small, compact muscle composed of transverse bundles. Surrounds and also lies between anterior ends of calami of rectrices. Attaches to rectrices and to combined insertion of M. lateralis caudae and M. lateralis coccygis.

The muscle is newly described in this study.

Mostly enclosed by combined slip of M. lateralis caudae and M. lateralis coccygis.

Origin and Insertion. Only functional attachment seems to be to rectrices, and no distinction can be made between origin and insertion.

Action. Expands rectrices by pulling tips of calami closer together.

Comparisons. In the Gruidae the muscle is well developed in Balearica but was not mentioned for Grus.

In the Rallidae the muscle is present in both Rallus and Fulica but is not so well developed in either as it is in Aramus.

Summary. In Aramus and Balearica the muscle is better developed than in Rallidae but it is unknown for Grus. The disposition is rather similar in the four genera examined.

Muscles of the Leg

112. M. extensor ilio-tibialis lateralis

Very large and thick, triangular sheet of muscle. Anterodorsal portion extensively aponeurotic, and large and somewhat triangular tendinous sheet occupies most of distal half. Covers most of side of thigh. Attaches to ilium, to M. extensor ilio-tibialis anterior, to M. gluteus profundus, to M. piriformis, to M. extensor ilio-fibularis, to M. vastus lateralis, to M. vastus medialis, to M. flexor cruris lateralis, to patellar tendon, to M. femoritibialis externus, to M. flexor perforans et perforatus digiti II, to M. peroneus longus, and to internal part of M. gastrocnemius.

Anterodorsal corner deep to M. extensor ilio-tibialis anterior and portion of distal end deep to M. flexor perforans et perforatus digiti II. Adjoins posterior edge of M. extensor ilio-tibialis anterior and anterodorsal corner of M. flexor crucis lateralis. Lies superficial to edges of previous two muscles. Completely covers M. vastus lateralis, and M. vastus medialis, and covers most of M. extensor ilio-fibularis, M. femoritibialis externus, M. iliacus, M. piriformis, and M. gluteus profundus.

Origin. Arises from entire iliac crest, by aponeurosis from entire anterior crest and anterior half of posterior iliac crest, and by mostly fleshy fibers from all but posterior 4 mm of posterior region of crest. Aponeurosis attaches strongly to superficial surfaces of M. gluteus profundus, and

M. piriformis and forms common origin with anterodorsal corner of *M. extensor ilio-fibularis*. Aponeurosis gives rise to fleshy belly at level of ventral edges of *M. gluteus profundus* and *M. piriformis*.

Insertion. Muscular bundles merge at different levels with large aponeurosis at distal end, and bundles from *M. vastus lateralis* and *M. vastus medialis* fuse with deep side of aponeurosis, which continues distad to form patellar tendon. At knee anterior edge of aponeurosis fuses with *M. extensor ilio-tibialis anterior*, and posterior edge fuses with tendon of *M. femortibialis externus* to insert on proximal edges of outer cnemial and rotular crests. *M. flexor perforans et perforatus digiti* II, *M. peroneus longus*, and *internal* part of *M. gastrocnemius* attach to tendon of insertion.

Action. Extends shank and simultaneously abducts leg and flexes femur posteriad.

Comparisons. In the Gruidae the muscle is similar (and agrees well with that of *Aramus*). A minor variation is present in the origin, which is partly fleshy near the posterior end in *Balearica* and *G. americana* but is entirely aponeurotic in *G. canadensis* (and *Aramus*). In both *Balearica* and *Grus* the anterodorsal corner of the origin is fused to *M. extensor ilio-tibialis anterior* (in *Aramus* it lies deep to that muscle). In *Balearica* the inserting tendon fuses with that of *M. femoritibialis externus*, but passes superficial to it in *Grus* (in *Aramus* the edges of the two tendons are continuous

with each other). In *Grus* this condition is uncertain, but *M. femoritibialis externus* apparently lies deep to the tendon of the present muscle.

In the Rallidae the anterior portion of the origin in *Rallus* is fused inseparately to *M. extensor ilio-tibialis anterior*, but in *Fulica* (and *Aramus*) this portion of the origin is separate and lies ddep to that muscle. In both rallids (but not in *Aramus*) a portion of the origin is from the dorsal side of the posterior iliac crest. In *Rallus* the connection to the posterior edge of *M. extensor ilio-tibialis anterior* is weak but much more extensive than in *Aramus*, and is intermediate in *Fulica*. In both rallids the extent of fusion to *M. vastus lateralis* and *M. vastus medialis* is less than in *Aramus*, and the fusion to the underlying *M. femoritibialis externus* is restricted to a small distal portion of the deep side (in *Aramus* the posterior edge of the tendon is continuous with the anterior edge of the tendon of *M. femoritibialis externus*).

Summary. The main variations are found in attachments to surrounding muscles. The connection to *M. extensor ilio-tibialis anterior* is more extensive in the Rallidae than in *Aramus* or Gruidae, but in the rallids the fusion to *M. vastus lateralis* and *M. vastus medialis* is less extensive than in the other two families. In Gruidae and in *Rallus* the anterodorsal corner is fused with *M. extensor ilio-tibialis anterior*, but is separate and deep to that muscle in *Aramus* and *Fulica*. In *Aramus* the aponeurosis of insertion is continuous

posteriorly with the inserting tendon of M. femoritibialis externus, but in Gruidae and Rallidae the aponeurosis is superficial to that tendon. The points of origin and insertion are similar in all five genera.

113. M. extensor ilio-tibialis anterior

Elongate and strap-like, medium-sized muscle. Located along anteromedial face of thigh and covers anterolateral portion of sacrum. Attaches to ilium, to M. extensor ilio-tibialis lateralis, to internal part of M. gastrocnemius, and to tibiotarsus.

Extreme anterodorsal corner deep to tendon of posterior part of M. latissimus dorsi. Posterior edge of belly deep to M. extensor ilio-tibialis lateralis, and distal end deep to internal part of M. gastrocnemius. Superficial at proximal end to portion of M. extensor ilio-tibialis lateralis, to M. gluteus profundus, and to M. iliacus. Belly covers some of most posterior Mm. intercostales on body wall. Distal portion of belly lies medial to M. ambiens and M. vastus medialis.

Origin. Arises fleshily from small triangular area at anterodorsal corner of sacrum and tendinously from median dorsal ridge along anterior fifth of length of ilium.

Insertion. Attaches mainly by strong aponeurosis to the anterior edge of proximal surface of tibiotarsus at point of origin of inner cnemial crest; also attaches fleshily to anterior edge of patellar tendon, and therefore, indirectly to M. vastus medialis and M. extensor ilio-tibialis

lateralis. Insertion lies deep to internal part of M. gastrocnemius, which arises partly from tendon.

Action. Extends shank, and at same time, flexes femur forward and upward.

Comparisons. In the Gruidae the posterior edge of the proximal end of the belly is fused to M. extensor ilio-tibialis lateralis (lies superficial to that muscle in Aramus). In Balearica and G. canadensis the origin is partly from the neural spine of the last dorsal vertebra, but in G. americana (and Aramus) it is only from the ilium. In G. canadensis the main origin is in common with M. latissimus dorsi from the same vertebra, but in the other two cranes (and Aramus) this origin is lacking or very minor (Hudson, 1937) stated that the origin in G. canadensis is only from the ilium. In Balearica the distal end overlaps the aponeurosis of M. extensor ilio-tibialis lateralis, but apparently in Grus it only fuses to the edge of the aponeurosis (as in Aramus).

In the Rallidae, but not in Aramus, there is strong connection to the posterior part of M. latissimus dorsi and to the last dorsal vertebrae. In Rallus the proximal end of the belly is fused to M. extensor ilio-tibialis lateralis, but in Fulica (and Aramus) it lies superficial to that muscle. In Rallus the connection to the anterior edge of the latter muscle is much more extensive than in Aramus, and somewhat more so than in Fulica.

Summary. In the Gruidae and in Rallus the proximal end is fused to M. extensor ilio-tibialis lateralis, but in

Aramus and Fulica it is superficial to that muscle. Part of the origin is from M. latissimus dorsi and the last dorsal vertebra in G. canadensis, Balearica, and the two rallids, but only in G. canadensis is this the main origin. The fusion of the belly to M. extensor ilio-tibialis lateralis is more extensive in Rallidae then in the non-rallids. Only in Balearica does the insertion overlap the aponeurosis of the latter muscle, and only in G. americana is the muscle fused to M. femoritibialis internus.

114. M. piriformis

Small, triangular muscle, tendinous in distal third. Located on side of proximal end of femur and on sacrum just posterodorsal to acetabulum. Attaches to sacrum, to femur, and to M. extensor ilio-fibularis.

Beddard (1898) noted the absence of this muscle in Aramus.

All but anterodorsal third deep to combined sheet of M. extensor ilio-tibialis lateralis and M. extensor ilio-fibularis. Connected to anterior edge of latter muscle, and contacts proximal end of M. vastus lateralis and insertion of M. iliacus. Superficial to posterior edge of M. gluteus profundus.

Origin. Arises mostly fleshily from small dorsal section of lateral face of ilium, dorsal to acetabulum; origin bordered dorsally by iliac crest. Posterior edge of origin fuses to M. extensor ilio-fibularis.

Insertion. Attaches strongly to very small oval scar on side of proximal end of femur, near proximal edge of origin of M. vastus lateralis; inserts by strong triangular tendon comprising slightly less than distal half of muscle.

Action. Abducts leg.

Comparisons. In the Gruidae the muscle in Balearica and G. canadensis (and Aramus) is nearly twice as wide at the proximal end as in G. americana. In the three gruids the origin is narrower, the belly thinner, and the insertion more elongate than in Aramus. This muscle has apparently been found previously in cranes only by Fisher and Goodman and Berger.

In the Rallidae the muscle is not fused to M. extensor ilio-fibularis (as it is in Aramus). In both rallids the distal tendon is wider than in Aramus, and the insertion is wider and oriented horizontally, covering portions of the insertions of M. iliacus and M. flexor ischio-femoralis (in Aramus the insertion is oriented vertically and does not cover any of either of these muscles).

Summary. The muscle is somewhat thinner in the Gruidae than in Aramus and the Rallidae. The muscle is considerably narrower in G. americana than in the other two cranes and in the non-gruids. The insertion in the Rallidae is wider and more vertically oriented than in the non-rallids. Only in Aramus does the belly fuse to M. extensor ilio-fibularis.

115. *M. gluteus profundus*

Medium-sized muscle, but very thick. Located on side of preacetabular ilium and on proximal end of femur. Attaches to ilium, to *M. iliacus*, to *M. extensor ilio-tibialis lateralis*, and to femur.

Entirely deep to aponeurosis of origin of *M. extensor ilio-tibialis lateralis* and fused to it in anterior half. Small portion of posterodorsal corner deep to *M. piriformis*. Superficial to proximal tip of *M. vastus medialis* and to all but lateral edge of *M. iliacus* and fused to it anteriorly.

Origin. Arises almost entirely fleshily, except for superficial fascis, from oval scar covering nearly all of preacetabular ilium. Origin bordered dorsally and anteriorly by anterior iliac crest and ventrally by small ridge along dorsal edge of *M. iliacus*.

Insertion. Inserts on proximal end of femur, on vertical line down center of lateral face. Attaches by short but thick aponeurosis that is formed at distal end of belly.

Action. Rotates anterior edge of thigh inward and abducts leg slightly.

Comparisons. In the Gruidae the belly in *Balearica* differs from that of *Aramus* in being fused to the entire length of *M. iliacus*, but in *Grus* the two muscles are apparently separate. In the cranes, and especially in *Balearica*, the scar of insertion is wider than that of *Aramus*. In *Balearica* the inserting tendon is superficial to the dorsal edge of the insertion of *M. iliacus*, but in *Grus* (and *Aramus*) it is

proximal to the latter muscle. In *Balearica* (and *Aramus*) the insertion is anterodorsal to the insertion of *M. piriformis*, but in *Grus* it is partly deep to the latter muscle.

In the Rallidae there is fleshy attachment in *Rallus* to the entire dorsal surface of *M. iliacus*, but in *Fulica* the two muscles are not connected at all. In both rallids, and especially in *Rallus*, the origin extends much further posteriorly than in *Aramus*, all the way to the portion of the ilium dorsal to the acetabulum. In *Fulica* a portion of the origin is from *M. spinalis thoracis*, which is exposed on the ilium, but in *Rallus* the latter muscle is covered by the ilium. In both rallids, (but not in *Aramus*) a small portion of the insertion is deep to *M. piriformis*, and a small portion is superficial to *M. iliacus*. In both rallids a considerable portion of the insertion is fleshy on the dorsal face of the neck of the femur (this insertion is lacking in *Aramus*).

Summary. In *Balearica* and *Rallus* the muscle is extensively fused to *M. iliacus*, but this area of fusion is much smaller in *Aramus* and is lacking in *Grus* and *Fulica*. In Rallidae the origin extends farther posteriorly on the ilium than in *Aramus* or Gruidae, and a portion of the insertion is fleshy on the dorsal side of the neck of the femur. In the non-rallids the insertion is restricted to the lateral face of the femur. In *Fulica* only, a portion of the origin is from *M. spinalis thoracis*.

116. M. "iliacus" (ilio-trochantericus anterior)

Medium-sized and uniformly flat muscle, triangular in dorsal view. Lies mostly deep and ventral to anterior portion of hip musculature. Attaches to ilium, to M. gluteus profundus, to M. vastus lateralis, and to femur.

Dorsomedial portion deep to M. gluteus profundus and fused to it anteriorly. Ventrolateral edge deep to M. extensor ilio-tibialis anterior and M. extensor ilio-tibialis lateralis. Superficial to M. ilio-costalis and Mm. intercostales of body wall. Superficial to proximal end of M. vastus medialis and to M. ilio-trochantericus medius.

Because of intimate relations of the muscle to other ilio-trochantericus muscles, it is probably more reasonable to follow Berger (1956a) and call it M. ilio-trochantericus anterior.

Origin. Arises by mixed tendinous and fleshy fibers from ventrolateral edge of preacetabular ilium, along ventral edge of origin of M. gluteus profundus.

Insertion. Extreme distal end of muscle becomes strongly tendinous and inserts on elongate, vertical scar on lateral side of proximal end of femur. Insertion contacts insertion of M. piriformis and furnishes part of origin of M. vastus lateralis.

Action. Rotates anterior side of leg inward.

Comparisons. In the Gruidae the entire dorsal surface of the muscle in Balearica is fused to the underside of M. gluteus profundus (in Aramus only the anterior portions of

the two muscles are fused), but in Grus there apparently is no fusion of the two. In the three cranes superficial fleshy fibers extend over the tendon to the insertion (in Aramus the insertion is entirely tendinous). In Balearica (and Aramus) a portion of M. vastus lateralis arises from the inserting tendon, but in Grus the two muscles do not overlap.

In the Rallidae the whole dorsal side of the muscle in Rallus is fused to M. gluteus profundus, but in Fulica there is no fusion at all. In both rallids the origin of the muscle extends much further posteriorly than in Aramus, all the way to the acetabulum. In both rallids the insertion is partly deep to that of M. gluteus profundus and partly in common with M. piriformis. Both rallids agree with Aramus in having a small portion of the origin of M. vastus lateralis arising from the inserting tendon.

Summary. Variation exists in the extent of fusion to M. gluteus profundus, the connection being very extensive in Balearica and Rallus, but intermediate in Aramus. Fusion is lacking in Grus and Fulica. Aramus resembles the rallids, and differs from the gruids, in having the insertion entirely tendinous. Other minor variations are found in the insertion.

117. M. ilio-trochantericus medius

This muscle is absent in Aramus, as previously reported by Mitchell (1901).

Comparisons. In the Gruidae the presence of the muscle in the cranes is apparently inconsistent. It is absent in the one specimen of Balearica, but it was reported present, but small, in this genus by Mitchell (1901). Fisher and Goodman found the muscle in G. americana, and Berger found it in G. canadensis, although only unilaterally in one specimen. It has been reported absent in Grus by Gadow (1893) and Hudson (1937). In Grus the muscle arises at the posterior edge of M. iliacus and inserts on the lateral face of the proximal end of the femur, just proximal to the insertion of M. iliacus. It functions as a rotator of the femur.

In the Rallidae the muscle is absent as reported for Fulica by Hudson (1937).

Summary. The muscle is absent in Aramus and Rallidae. Its presence in Gruidae is apparently quite variable, ranging from complete absence in Balearica and Grus, through small size and/or unilateral presence in Balearica and G. canadensis, to well developed and bilateral presence in G. americana.

118. M. vastus lateralis

Bulky medium-sized muscle, elongately oval in lateral view. Located on side of shaft of femur. Attaches to femur, to M. vastus medialis, to M. extensor ilio-tibialis lateralis, to patellar tendon, and indirectly to M. femoritibialis externus and M. extensor ilio-tibialis anterior.

Completely deep to M. extensor ilio-tibialis lateralis. Muscle lies posterior and superficial to edge of M. vastus

medialis and anterior and superficial to anterior end of *M. caudofemoralis*. Lies just anterior to *M. extensor iliofibularis* and adjoins insertion of *M. iliacus*.

Origin. Arises fleshily from lateral surface of most of proximal half of femoral shaft and from small portion of insertion of *M. iliacus*. Area of origin continuous anteriorly with area of origin of *M. vastus medialis*.

Insertion. Attaches indirectly onto patellar tendon and rotular crest of tibiotarsus, as result of fusion of distal end to underside of aponeurosis of *M. extensor iliotibialis lateralis*, and, anteriorly, to belly of *M. vastus medialis*. Also inserts indirectly onto inner cnemial crest of tibiotarsus, as result of indirect distal fusion with *M. femoritibialis externus*.

Action. Abducts leg, extends shank, and flexes femur posteriad.

Comparisons. In the Gruidae the muscle is larger than in *Aramus* and has a much larger portion arising from the area of the femur along the posterior edge of *M. femoritibialis externus*. The origin in *Balearica* (and *Aramus*) extends nearly the entire length of the shaft of the femur, but in *Grus* it extends "to the distal third of the femoral length" (Fisher and Goodman, 1955). The insertion is similar in all three cranes and *Aramus*.

In the Rallidae the muscle and its origin in *Rallus* are similar to those of *Aramus*, but in *Fulica* the belly is wider, and a much larger portion of the insertion attaches along the

posterior edge of M. femoritibialis externus. Both rallids differ from Aramus in having the fusion of the belly to M. extensor ilio-tibialis lateralis less extensive and in lacking connection to M. vastus lateralis.

Summary. This muscle in the gruids is considerably larger than in Aramus or Rallus and slightly larger than in Fulica. In the cranes and in Fulica much of the origin arises from the femur posterior to M. femoritibialis externus, but this portion of the origin is lacking in Aramus and Rallus. The origin in Grus does not extend so far distad as in Balearica or the non-gruids. The fusion of the belly to M. extensor ilio-tibialis lateralis is much less extensive in Rallidae than in Aramus and the Gruidae.

119. M. vastus medialis

Elongate but very thick muscle, somewhat rounded along anterior edge. Located along anterior face of length of femur. Attaches to femur, to M. extensor ilio-tibialis lateralis, to M. extensor ilio-tibialis anterior, to M. vastus lateralis, to internal part of M. gastrocnemius, to patellar tendon, and to patella.

Lies deep to M. gluteus profundus, to M. iliacus, to M. extensor ilio-tibialis lateralis, and to internal part of M. gastrocnemius. Lies posterior to most of length of M. extensor ilio-tibialis anterior and fuses with anterior edge of M. vastus lateralis. Superficial to M. ambiens and to some of most posterior of Mm. intercostales.

Origin. Arises from nearly whole anterior face of shaft of femur, tendinously at proximal end and fleshily throughout remainder of attachment. Posteromedial edge of origin merges with origin of _M_. _vastus_ _lateralis_.

Insertion. In about middle of thigh belly becomes intimately fused to _M_. _vastus_ _lateralis_ and _M_. _extensor_ _iliotibialis_ _lateralis_. All three insert together by way of patellar tendon, although some fleshy fibers of _M_. _vastus_ _medialis_ continue distad to insert directly on patella.

Action. Extends shank.

Comparisons. In the Gruidae the only variation found in this muscle is in _Grus_, in which fleshy fibers do not always extend to the patella as they do in the one specimen of _Balearica_ (and in _Aramus_).

In the Rallidae this muscle is somewhat thicker than in _Aramus_, but is otherwise quite similar.

Summary. In Rallidae the muscle is somewhat thicker than in _Aramus_ or Gruidae, but is otherwise essentially the same in all three families.

120. _M_. _extensor_ _ilio-fibularis_

Large muscle, wide and thin at dorsal end, becoming narrower but more thickly rounded toward ventral end; narrows abruptly at knee to form strong, rounded tendon that passes through ligamentous guide loop. Located mainly on side of posterior half of thigh, but passes posterior to knee and onto posterolateral portion of upper region of shank. Attaches

to ilium, to _M_. _extensor_ _ilio-tibialis_ _lateralis_, and to fibula.

Mostly deep to _M_. _extensor_ _ilio-tibialis_ _lateralis_, but distal end also deep to external part of _M_. _gastrocnemius_ and to _M_. _flexor_ _perforans_ _et_ _perforatus_ _digiti_ II. Superficial to portion of _M_. _piriformis_, to _M_. _caudofemoralis_, to _M_. _flexor_ _ischiofemoralis_, to _M_. _adductor_ _superficialis_, and to anterior edge of _M_. _flexor_ _cruris_ _lateralis_. Distal end passes lateral to lateral head of _M_. _flexor_ _perforatus_ _digiti_ IV.

Origin. Arises by mixed fleshy and tendinous components from narrow area along underside of posterior iliac crest, from level of posterior corner of antitrochanter to point 9 mm from posterior tip of ilium. Area of origin contacts origin of _M_. _piriformis_ anteriorly and origin of _M_. _flexor_ _cruris_ _lateralis_ posteriorly. Anterior third of origin partially common to _M_. _extensor_ _ilio-tibialis_ _lateralis_ and extends over posterior two-thirds of _M_. _piriformis_.

Insertion. Inserts by strong tendon onto small tubercle of anterolateral edge of fibula, at level of center of fibular crest of tibiotarsus. Inserting tendon forms posterior to knee by abrupt narrowing of belly, and this rounded tendon then passes through ligamentous loop to fibula. Most proximal arm of ligamentous loop arises from lateral face of distal end of femoral shaft, deep to _M_. _femoritibialis_ _externus_. Distal arm of loop passes lateral to present tendon and divides, with one branch attaching strongly to tendon of origin

of _M_. _flexor perforans et perforatus digiti_ II and the other to the external part of _M_. _gastrocnemius_.

Action. Flexes shank and abducts leg.

Comparisons. In the Gruidae the belly is thickest in the proximal half, becoming thinner distally (in _Aramus_ the belly is thin proximally but becomes thicker distally). In _Grus_ the origin extends to the posterior tip of the ilium dorsal to _M_. _flexor cruris lateralis_, but in _Balearica_ (and _Aramus_) the origin ends well anterior to the posterior end of the ilium and does not overlie the latter muscle. In _Balearica_ (and _Aramus_) the distal arm of the ligamentous guide loop branches, and one branch attaches to the external part of _M_. _gastrocnemius_ while the other attaches to _M_. _flexor perforans et perforatus digiti_ II. Both these branches apparently correspond to the vinculum of _Grus_, which attaches to several flexor muscles and sometimes to the fibula. in _G. canadensis_. The distal arm of the loop has an attachment to the femur in _Grus_ only.

In the Rallidae the belly is narrower and of a somewhat more uniform thickness, and the origin is narrower than in _Aramus_. The insertion is alike in both rallids and is similar to that of _Aramus_. The guide loop is also essentially uniform, but in _Rallus_ the branch of the distal arm attaching to the tendon of _M_. _gastrocnemius_ may still be traced to the femur, whereas in _Fulica_ (and _Aramus_) it becomes inseparably fused.

Summary. The belly has a somewhat different shape in each family. It is narrowest in Rallidae, widest in Gruidae,

intermediate in _Aramus_. The extent of the origin varies directly with the width of the belly. The distal arm of the guide loop attaches to the femur in _Grus_ and in _Rallus_, but in _Aramus_, _Balearica_, and _Fulica_ it does not. Some other specializations of the guide loop occur only in _Grus_. The insertion is similar in all five genera.

121. _M. flexor cruris lateralis_

Large muscle composed of one main head and two smaller accessory heads. Main head somewhat elongate, thick in posterodorsal half but flattened in anteroventral half. Proximal accessory head wide and flat, joining distal end of main head, and distal accessory head small, joining posterodistal edge of other accessory head. Main head lies in posterolateral portion of thigh, and two distal heads located in posterior region of knee and upper shank. Whole complex attaches to ilium, to _M. flexor cruris medialis_, to _M. transverso-analis_, to femur, and to _M. gastrocnemius_.

Anterodorsal corner of main head deep to _M. extensor ilio-tibialis lateralis_, and middle of its belly deep to _M. extensor ilio-fibularis_. Proximal accessory head partly deep to _M. femoritibialis externus_ and to proximal arm of ligamentous loop of _M. extensor ilio-fibularis_. Distal accessory head lies between internal and medial heads of _M. gastrocnemius_. Main belly superficial to posterior edges of _M. caudofemoralis_, _M. flexor ischio-femoralis_, and _M. adductor superficialis_ and to lateral face of _M. flexor cruris medialis_. Proximal accessory head also superficial to _M._

adductor superficialis and to small portion of M. adductor profundus.

Origin. Main head arises by fleshy and tendinous fibers from underside of posterior 9 mm of posterior iliac crest and tendinously from posterior edge of junction of M. flexor cruris medialis and M. transverso-analis. Proximal accessory head arises from narrow area on posterolateral edge of distal end of femur, extends into lateral region of popliteal area and merges with origin of distal accessory head, which arises from remainder of popliteal area and from proximal edge of internal condyle. Fibers of proximal accessory head pass posterodorsad to end of connective tissue raphe that forms at distal ends of bundles of main head; raphe continues distad as tendon, which fuses with posterior edge of distal accessory head.

Insertion. Tendon from raphe passes, in company with distal accessory head, laterally by M. flexor cruris medialis, sends weak vinculum to lateral face and small tendon to posterior edge of M. flexor cruris medialis, and then fuses with posterior edge of internal part of M. gastrocnemius. Distal accessory head also fuses entirely with internal head of M. gastrocnemius at distal end of belly of latter muscle. Origin of proximal accessory part functions also as an insertion.

Action. Flexes femur posteriad, flexes shank, and aids in extending tarsus.

Comparisons. In the Gruidae the anteroventral region of the belly in Balearica is even more abruptly flattened

than in Grus (or Aramus). In Grus the origin is wider than in Balearica (or Aramus) and is located partly deep to M. extensor ilio-fibularis. In Balearica (and Aramus) the origin adjoins the posterior edge of that muscle, but is not deep to it. In all three cranes the origin differs from that of Aramus in being more extensive and in including attachment to a portion of the body wall. Only in Balearica, does the muscle completely cover the entire posterior edge of M. flexor cruris medialis and attach extensively to it. In Balearica (and Aramus) the inserting tendon extending from the raphe attaches to M. flexor cruris medialis but inserts mainly on the medial head of M. gastrocnemius. In Grus this insertion is usually only on M. flexor cruris lateralis. The insertion of the distal accessory head in the three cranes is similar to that of Aramus.

In the Rallidae Rallus has the tendon of the proximal accessory part arising from the raphe and inserting mainly on the external head of M. gastrocnemius, but in Fulica and Aramus it inserts on the internal head. In both rallids as in Aramus the tendon of the distal accessory head attaches to M. flexor cruris medius and fuses to the internal head of M. gastrocnemius.

Summary. The belly and origin are wider in Gruidae than in Aramus and Rallidae. In Grus the insertion of the tendon that extends from the raphe is mainly on M. flexor cruris medialis, but in Balearica and the non-gruids it inserts mainly on the internal head of M. gastrocnemius. In Rallus the insertion of the tendon of the distal accessory head is

on the external head of *M. gastrocnemius*, but in *Fulica* and the non-rallids it inserts on the internal head of that muscle.

122. *M. flexor cruris medialis*

Medium-sized and rather bulky band of muscle with irregular shape, but thickest in posteroventral region. Small strap-like head separates from deep side of main belly at proximal end. Located in posteromedial region of thigh. Attaches to ischium, to ischio-pubic ligament, to ligament along posterior border of ischium, to *M. transverso-analis*, to *M. gastrocnemius*, to *M. flexor cruris lateralis*, and to tibiotarsus.

Almost completely deep to *M. flexor cruris lateralis*. Proximal end lies just posterior to *M. flexor ischiofemoralis* and *M. adductor superficialis*; distal end passes between *M. flexor cruris lateralis* and internal head of *M. gastrocnemius*, with some connection to both. Superficial to *M. transverso-analis* and *M. internal oblique*.

Origin. Arises mostly fleshily from posteroventral edge of ischium and ischio-pubic ligament. Small deep head arises from separate area on side of posteroventral portion of lateral face of pubis, about 3 mm from posterior end. Small tendon arises near junction of posterior edges of ilium and ischium. Posterodorsal corner of origin has some connection to *M. flexor cruris lateralis* and to *M. transverso-analis*.

Insertion. Belly narrows posterior to knee, forms wide but very thin aponeurosis, and inserts on narrow line along

anteromedial edge of proximal end of shaft of tibiotarsus. Insertion connects strongly to internal head of M. gastrocnemius and less strongly, by weak vinculum, to tendons of M. flexor cruris lateralis.

Action. Flexes thigh and rotates posterior edge inward and adducts leg.

Comparisons. In the Gruidae the anterodorsal corner in Balearica and Aramus is superficial to a corner of M. adductor profundus, but in Grus it is deep to that corner of the latter muscle. In Balearica the belly is completely deep to M. flexor cruris lateralis and is uniformly thin; in Grus (and Aramus) the posteroventral portion of the belly is exposed (and in Aramus this portion is much wider than the covered portion). All three cranes differ from Aramus in having the portion of origin from the pubis more extensive and in having it not extend to the posterior end of the bone. The cranes also differ from Aramus in lacking the separate small, deep head and small tendon. In Balearica and G. canadensis (and Aramus) a vinculum from the inserting tendon of M. flexor cruris lateralis attaches to the tendon of this muscle, but in G. americana this connection may be by a vinculum or by a direct insertion on the tendon. In Balearica (and Aramus) the inserting tendon is intimately connected to the internal head of M. gastrocnemius. In G. americana there may be connections to both the internal and medial heads, but in G. canadensis the connection is only to the medial head. In the three cranes the insertion is on the posteromedial edge of the tibiotarsus (in Aramus it inserts on the anteromedial edge). The

level of the insertion varies, being located farther distad in G. americana than in G. canadensis or Balearica (or Aramus).

In the Rallidae the belly in Fulica is considerably wider than in Rallus (or Aramus) and is located partly deep to M. adductor profundus. In Rallus the posteroventral region of the belly is thick (as in Aramus), but in Fulica the belly is uniformly thin. The rallids differ from Aramus in lacking the small deep head and tendon, as well as the vinculum from M. flexor cruris lateralis to the inserting tendon. In Rallus the tendon does not connect to the tendon of the distal accessory head of the latter muscle, but in Fulica (and Aramus) there is some connection to both accessory heads. The insertion in both rallids is like that of Aramus.

Summary. The belly is wider in Fulica than in Rallus or the non-rallids. Only in Grus and Fulica is there a portion of the belly deep to M. adductor profundus. The belly has a thickened region posteroventrally in Aramus, Grus, and Rallus, but not in Balearica or Fulica. Aramus and the gruids have a portion of the origin from the pubis, but in the rallids this origin is lacking. Only in Aramus is there a small tendon of origin dorsally, and is the portion arising from the pubis separate from the main belly. Aramus and the gruids differ from the rallids in receiving a vinculum from M. flexor cruris lateralis. The insertion in Aramus and Rallidae is on the anteromedial edge of the tibiotarsus, but in Gruidae it is on the posteromedial edge.

123. M. caudofemoralis

Small and short, but widely band-like, with small tendinous area in middle of anterodorsal edge of belly. Composed entirely of ilio-femoralis (accessory) division. Located in deep portion of upper thigh, just posteroventral to hip joint. Attaches to ilium and to femur.

The absence of the caudi-femoralis part in Aramus has been found by Beddard (1898) and mentioned and figured by Mitchell (1901), but his large "area of tendinous degeneration" is very small in my specimens and seems merely the result of pressure from the overlying M. ilio-fibularis. I find the muscle to be consistently wider than in his illustration (p. 648).

Extreme distal end deep to M. vastus medialis and extreme proximal end deep to M. flexor cruris lateralis, but most of belly deep to M. flexor ilio-fiburaris. Belly superficial to most of M. flexor ischiofemoralis and to anterodorsal corner of belly of M. adductor superficialis.

Origin. Arises by mixed fibers from elongate area of postacetabular ilium, just ventral to posterior iliac crest and to portions of origins of M. flexor cruris lateralis and M. extensor ilio-fibularis. Line of origin extends for about 15 mm, beginning about 2 mm from posterior edge of ilium.

Insertion. Attaches fleshily to small, lacrimiform area on posterior face of shaft of femur, about 18 mm from proximal edge of trochanter.

Action. Flexes femur posteriad.

Comparisons. In the Gruidae the caudi-femoralis part is lacking in Balearica (and Aramus), but both parts are usually present in Grus. In G. americana the caudi-femoralis part may occasionally be missing, and the ilio-femoralis part may be divided into two parts. In Grus the caudi-femoralis part is slender. It arises from the pygostyle in G. americana but is from fascia in that area in G. canadensis. It inserts on the femur distal to the insertion of the ilio-femoralis part in G. americana, deep to it in G. canadensis. In the three cranes the ilio-femoralis part is thinner and more highly aponeurotic than in Aramus. In Balearica, and G. canadensis (and Aramus) the insertion of the ilio-femoralis part is distal to the insertion of M. flexor ischio-femoralis, but in G. americana it inserts proximal to, or at the same level as, the latter muscle. The insertion of the ilio-femoralis part in Balearica (and Aramus) is on the posterior face of the femur, but on the lateral face in Grus.

The condition of this muscle in Balearica agrees with the descriptions of Beddard (1898) and Mitchell (1901).

In the Rallidae both parts of this muscle are present in the two rallids. In both the ilio-femoralis part is slightly larger than in Aramus. The origin of this part in Rallus resembles that of Aramus in arising from the ventral edge of the greatly expanded posterior iliac crest. In Fulica this part arises from a large triangular area comprising almost the posteroventral half of the lateral side of the postacetabular sacrum (in Aramus most of this area is utilized by

attachments of _M._ _flexor ischio-femoralis_ and _M._ _flexor cruris lateralis_). The insertion of this part is similar to _Aramus_ in both rallids. The _caudi-femoralis_ part (absent in _Aramus_) is large in both rallids, being as wide as the _ilio-femoralis_ part in _Rallus_ and two-thirds as wide in _Fulica_. In both rails it originates tendinously from the posteroventral surface of the pygostyle and fleshily from fascia on the underside of the rectrices, deep to _M._ _depressor coccygis_. It inserts by very narrow tendon at ventral edge of insertion of _ilio-femoralis_ part. In _Fulica_ the tendon fuses to the other part, but it remains separate in _Aramus_.

Summary. Both parts of this muscle are usually present in _Grus_ and Rallidae, but in _Aramus_ and _Balearica_ only the _ilio-femoralis_ (accessory) part is present. In Rallidae the _caudi-femoralis_ part is much wider than in Gruidae and is fleshy except at its two extremities. In Gruidae this part is very narrow and is tendinous in the posterior third. In the two rallids and _G._ _canadensis_ the insertion is adjacent to that of the _ilio-femoralis_ part, but removed from it in _G._ _americana_. The _ilio-femoralis_ part has a larger origin in _Fulica_ than in _Rallus_ or the non-rallids. In _G._ _americana_ this part may sometimes be composed of two parts. In _G._ _americana_ the insertion of this part is distal to the insertion of _M._ _flexor ischiofemoralis_, but in the other two cranes and the non-gruids the insertion is proximal to the insertion of the latter muscle.

124. _M. flexor ischiofemoralis_

Small, flattened muscle, somewhat oval-shaped in lateral view; distal portion of belly covered by silvery fascia. Located on posterolateral portion of ischium. Attaches to ilium, to ischium, and to femur.

Most of belly deep to _M. caudofemoralis_ but also partly deep to _M. piriformis_, _M. extensor ilio-fibularis_, and _M. flexor cruris lateralis_. Superficial to portions of _M. adductor superficialis_ and _M. obturator internus_ and _M. obturator externus_.

Origin. Arises fleshily from most of lateral surface of ischium, including portion forming floor of ilio-ischiatic fenestra, and from a portion of ilium posterior to fenestra. Origin bordered dorsally by origins of _M. caudofemoralis_ and _M. extensor ilio-fibularis_ and ventrally by origins of _M. flexor cruris medialis_ and _M. adductor superficialis_.

Insertion. Attaches strongly by wide tendon to small, triangular area on lateral face of proximal end of shaft of femur. Area of insertion lies posterior to insertion of _M. piriformis_ and lies completely deep to distal end of that muscle.

Action. Flexes femur posteriad and rotates posterior edge of thigh inward.

Comparisons. In the Gruidae this muscle is essentially the same as in _Aramus_, except for some differences in the relationship to the insertion of _M. caudofemoralis_. In _G. americana_ only, the insertion is distal to, or even with,

the insertion of the *ilio-femoralis* part of that muscle.

In the Rallidae the muscle in *Rallus* (and *Aramus*) is wider and longer than in *Fulica*. In *Rallus* it arises from the posteroventral region of the lateral face of the sacrum, and in *Fulica* it originates from a small area just postero-ventral to the ilio-ischiatic fenestra. In both rallids, and especially in *Rallus*, the muscle differs from that of *Aramus* in passing over the area of the sacrum posterior to the fenestra. The insertion in both rallids is like that of *Aramus*.

Summary. The muscle in *Fulica* is narrower and shorter than in *Rallus* and the non-rallids. The origin is rather similar in *Aramus* and Gruidae, but it is in an entirely different location in each of the two rallids.

125. *M. adductor superficialis*

Medium-sized, thick sheet of muscle, triangular in lateral view. Located on posterior side of femur. Attaches to ischium, to ischio-pubic ligament, and to femur.

Belly mostly deep to *M. flexor ilio-fibularis*, but posterior edge deep to *M. flexor cruris lateralis*. Dorsal end deep to *M. flexor ischio-femoralis* and *M. caudofemoralis*, and ventral end deep to *M. femoritibialis externus*. Superficial to all but posterior edge of *M. adductor profundus*.

Origin. Originates by mixed fleshy and tendinous fibers from small section of ventral edge of lateral face of ischium, and small portion of ischio-pubic ligament between origins of *M. flexor cruris lateralis* and *M. adductor profundus*. Narrow

Narrow line of tendinous origin continues anteriad, dorsal to origin of latter muscle, almost to obturator foramen. Origin bordered dorsally by area of origin of _M. flexor ischiofemoralis_.

Insertion. By fleshy fibers onto elongate area, about 40 mm long, on posterior face of shaft of femur; attachment extends from point 31 mm distal to proximal edge of trochanter to popliteal area near distal end. Insertion bordered laterally by origins of _M. vastus lateralis_, _M. femoritibialis externus_, and by proximal accessory head of _M. flexor cruris lateralis_. Bordered medially by insertion of _M. adductor profundus_.

Action. Adducts thigh and flexes it posteriad.

Comparisons. In the Gruidae the origin is partly from the pubis, as well as from the ischium, and from the section of the ischio-pubic ligament between the two (in _Aramus_ the origin is restricted to the ischium and a small dorsal portion of the ligament). In _Balearica_ (and _Aramus_) the origin is aponeurotic in at least the anterior third, but fleshy fibers are present throughout in _Grus_. Only in _Balearica_, is the posterior region of the origin partially common to the origin of _M. adductor profundus_. The insertion is similar in all three cranes (and _Aramus_).

In the Rallidae the muscle is somewhat narrower than in _Aramus_. In _Fulica_ the posterior edge is superficial to _M. flexor cruris medialis_, but in _Rallus_ these two muscles do not overlap. In both rallids the origin is composed of mixed

fibers and is partly fused to _M. flexor cruris medialis_ (in _Aramus_ the anterior portion of the origin is tendinous, and there is no fusion with _M. flexor cruris medialis_). In both rallids the insertion is narrower than in _Aramus_, and in _Fulica_ it is partly in common with _M. adductor profundus_.

Summary. The belly is narrower in Rallidae than in _Aramus_ and Gruidae. _Aramus_ and the rallids have the origin essentially restricted to the ischium, but the origin in the gruids is partly from the pubis. In _Aramus_ and _Balearica_ a large portion of the origin is aponeurotic, but in _Grus_ and Rallidae fleshy fibers are present throughout. In _Balearica_ only, the origin is partially common to _M. adductor profundus_. In _Fulica_ only, the insertion is in common with that muscle.

126. _M. adductor profundus_

Sheet-like, triangular muscle; mostly bulky and fleshy, but posterodorsal corner composed of thin aponeurosis. Lies on inner side of posterior region of thigh. Attaches to ischium, to ischio-pubic ligament, to pubis, and to femur.

Almost entirely deep to _M. adductor superficialis_, but dorsal tip deep to _M. flexor ischiofemoralis_, and posterior edge deep to _M. flexor cruris medialis_. Dorsal tip contacts _M. obturator externus_.

Origin. Arises by mixed fleshy and tendinous fibers from elongate area including ventral edge of lateral face of ischium ventral to ilio-ischiatic fenestra, adjacent region of ischio-pubic ligament, and adjacent dorsal half of lateral face of portion of pubis lying ventral and just

posterior to obturator foramen. Origin continues posteriad as aponeurosis arising from line passing to ventral edge of pubis and continuing to origin of *M. flexor cruris medialis.*

Insertion. Edge of belly next to femur forms very short aponeurosis, by which muscle inserts on narrow line down length of posterior face of shaft of femur. Insertion extends along entire medial edge of insertion of *M. adductor superficialis* and is bordered medially by origin of *M. femoritibialis internus*.

Action. Adducts thigh and flexes it posteriad.

Comparisons. In the Gruidae the aponeurotic posterodorsal section of the muscle is smaller than in *Aramus*, and in *Grus* it is apparently absent. In *G. americana* a "heavy layer of tendon" (Fisher and Goodman, 1955) covers the medial surface of the belly. This may be the same as the "glistening muscular fascia" (Berger, 1956a) on this surface in *G. canadensis*; in *Balearica* (and *Aramus*) a strong fascia is present in this area, but it is not particularly well developed. In *Balearica* (and *Aramus*) at least the posterior third of the origin is entirely aponeurotic, but in *G. americana* fleshy fibers arise along with the aponeurosis, and in *G. canadensis* the origin is entirely fleshy. In the three cranes the posterior portion of the origin is from portions of the ischium and ischio-pubic ligament, as well as from the pubis (in *Aramus* this portion of the origin is only from the pubis). In *Balearica* only, the most posterior portion of the origin is common to *M. adductor superficialis*.

In the Rallidae the posterodorsal corner of the muscle has a large aponeurotic area (as in Aramus). The origin in Rallus (and Aramus) is partly from the ischium and ischio-pubic ligament, but in Fulica it arises only from the pubis. Other features in both rallids are similar to those of Aramus, except that in Fulica the insertion is in common with M. adductor superficialis. In Rallus, but not in Fulica (or Aramus), there is fleshy connection to M. femoritibialis internus.

Summary. In Balearica and the non-rallids the posterodorsal corner of the muscle is aponeurotic, but in Grus this portion is fleshy. In G. americana only, the fascia on the medial face is very heavy. In Balearica and the non-rallids a large posterior portion of the origin is entirely aponeurotic, but in Grus fleshy fibers are present throughout. In Gruidae the posterior region of the origin is partly from the ischium and ischio-pubic ligament, but in Aramus and Rallidae this portion is restricted to the pubis. In Fulica only, the entire origin is restricted to the pubis. In Balearica only, the origin is partly in common with M. adductor superficialis, and in Fulica only, the insertion is in common with the same muscle.

127. M. ambiens

Very flat muscle, composed of small lanceolate belly that gives rise to narrow but strong tendon at distal end. Belly located on anteromedial portion of full length of thigh. Attaches to pectineal process, to M. flexor perforatus

digiti IV, to M. flexor perforatus digiti III, and to M. flexor perforatus digiti II.

Superficial in medial view to other thigh muscles. Deep at distal end to M. extensor ilio-tibialis lateralis, to patellar tendon, and to portions of perforated toe flexors.

Origin. Arises by small tendon from lateral tip of pectineal process.

Insertion. At distal end of femur belly gives rise to narrow, band-like tendon that passes from medial side of thigh to lateral surface of knee just beneath patellar tendon. Tendon then passes distad along side of proximal end of fibula, beneath inserting tendon of M. extensor ilio-fibularis, and merges with origins of portion of M. flexor perforatus digiti II, lateral head of M. flexor perforatus digiti III, and M. flexor perforatus digiti IV.

Action. Aids in flexing digits II, III, and IV.

Comparisons. In the Gruidae the origin is "widely fleshy," but in G. canadensis it is partly or entirely tendinous and is entirely tendinous in Balearica (and Aramus). In the three cranes the belly extends along the proximal two-thirds of the thigh (in Aramus it extends to the knee). In G. americana the tendon of insertion contributes directly to the origin of the deep head of M. flexor perforatus digiti II and indirectly to the origins of M. flexor perforatus digiti IV and lateral head of M. flexor perforatus digiti III. In Balearica (and Aramus) the tendon connects directly to all three muscles. In G. canadensis the insertion tendon usually

connects only to the lateral head of _M_. _flexor_ _perforatus_ _digiti_ III, but it may sometimes have a minor connection to _M_. _flexor_ _perforatus_ _digiti_ II.

In the Rallidae, especially in _Fulica_, the belly of the muscle differs from that of _Aramus_ in being bipinnate and wider. In the rails and _Aramus_ the belly extends nearly to the knee joint. In both rallids the origin is wide and fleshy and extends from the anterior face of the pectineal process to the dorsolateral border of the pubis below the obturator foramen (in _Aramus_ the origin is tendinous and restricted to a small area on the pectineal process). The inserting tendon in both rallids connects to the same toe flexors as in _Aramus_, although these connections are more extensive in _Fulica_.

Summary. This muscle is wide and bipinnate in Rallidae but is narrow and not bipinnate in _Aramus_ and Gruidae. The belly is considerably shorter in Gruidae than in _Aramus_ or Rallidae. The origin is wide and fleshy in _G_. _americana_ and Rallidae but is narrow and wholly or partly tendinous in _G_. _canadensis_, _Balearica_, and _Aramus_. In the two species of _Grus_ the insertion is on a single (but different) toe flexor. In _Balearica_ and the non-gruids the inserting tendon attaches intimately to three toe flexors.

128. _M_. _femoritibialis internus_

Small and elongate, somewhat rounded muscle, widest at distal end. Structure essentially bipinnate, but partially

separated into inner and outer heads. Lies along postero-medial face of femur. Attaches to femur, to patellar tendon, to M. gastrocnemius, and to tibiotarsus.

In medial view partly deep to M. psoas, M. extensor ilio-tibialis anterior, M. vastus medialis, M. ambiens, and M. gastrocnemius. In same view, partly superficial to M. adductor profundus.

Origin. Arises fleshily from elongate area occupying most of medial face of shaft of femur. Area of origin extends from insertion of M. psoas at proximal end, barely onto medial face of internal condyle at distal end; bordered posteriorly by insertion of M. adductor profundus on posterior intermuscular line and anteriorly by origin of M. vastus medialis.

Insertion. By strong tendinous attachment onto antero-medial edge of proximal end of tibiotarsus, just postero-medial to scar of insertion of M. extensor ilio-tibialis anterior. Two separate tendons are identifiable from inner head and one from outer head, but all fuse at insertion. Wide vinculum extends from tendon to fuse with edge of patellar tendon; internal head of M. gastrocnemius arises partly from tendon.

Action. Extends and adducts shank, and rotates its anterior edge inward.

Comparisons. In the Gruidae the muscle in Balearica, and sometimes in G. canadensis, is partially divided into three heads; the third head represents a separate portion of

the distal end of the inner head. In G. americana (and Aramus), and sometimes in G. canadensis, the muscle is partially divided into two heads. In Grus the dorsal extent of the origin is varied; it may extend into the proximal fifth of the femur, or it may be limited to the distal half (Gadow, 1893; Grus of unknown species). In Balearica (and Aramus) the origin extends into the proximal fifth. In Balearica (and Aramus), and sometimes in G. canadensis, three tendons are present. In G. canadensis (and Aramus) they fuse to insert as one, but in Balearica the tendon from the anterodistal portion of the muscle passes deep to the others and inserts separately just posterior to them. Only one tendon is described for G. americana. In Balearica (and Aramus) there is no connection of the tendons to any flexor muscles of the shank, but in Grus these connections are present.

In the Rallidae the muscle is divided into three distinct and mostly separate heads (in Aramus it is comprised of only two heads). In Rallus, but not in Fulica (or Aramus) the outermost head has fleshy connection to the inner side of M. adductor profundus. In both rallids the origin extends into the proximal one-eighth of the shaft of the femur (in Aramus it extends into the proximal one-seventh). In both rallids each head inserts separately, with the tendon from the most anterior head having the most posterior insertion, and vice-versa (in Aramus this crossing of tendons is indicated, but all tendons are fused as one at the insertion). In Fulica (and Aramus) a strong vinculum connects this muscle

to the patellar tendon; in *Rallus* the vinculum is very small and weak.

Summary. Three separate heads of this muscle are evident in all except *Aramus* and some specimens of *G. canadensis*, in which there are two heads. The area of origin is longest in Rallidae and somewhat shorter in *Aramus*; in Gruidae the length is varied but generally shorter than in *Aramus*. In *Aramus* and *Grus* only one tendon forms the insertion, but in *Balearica* two are present, and in Rallidae, three. Only in *Grus* does the insertion connect to some of the flexors of the shank, and only in *Rallus* is the wide vinculum to the patellar tendon lacking.

129. *M.* "*femoritibialis externus*" (external head of *M. vastus lateralis*)

Medium-sized and somewhat flattened triangular muscle with bipinnate belly. Located on side of lower thigh and knee. Attaches to femur, to *M. extensor ilio-tibialis lateralis*, to *M. flexor perforans et perforatus digiti* II, to *M. peroneus longus* and to tibiotarsus.

Berger (1956a) considers this muscle as an external head of *M. vastus lateralis*.

Belly completely deep to, and fused to, *M. extensor ilio-tibialis lateralis*, and *M. vastus lateralis*. Distal tendon partly deep to origins of *M. flexor perforans et perforatus digiti* II and to *M. peroneus longus*. Superficial to proximal attachment of guide loop for *M. extensor ilio-fibularis* and to parts of *M. adductor superficialis* and *M. flexor cruris lateralis*.

Origin. Arises fleshily from elongate area along side of distal half of shaft of femur.

Insertion. Attaches to proximal edge of outer cnemial crest by strong aponeurosis formed by converging fleshy fibers and by fusion with tendon of _M. extensor ilio-tibialis lateralis_. Insertion continuous with latter muscle, and indirectly, with _M. vastus lateralis_. _M. flexor perforans et perforatus digiti_ II and _M. peroneus longus_ attach fleshily to superficial surface of tendon. Small tendinous sheet connects to medial head of _M. gastrocnemius_.

Action. Extends shank.

Comparisons. In the Gruidae (as in _Aramus_) the main insertion is on the outer cnemial crest. A second insertion, on the patellar tendon, is accomplished in _Balearica_ (and _Aramus_) by fusion with the distal aponeurosis of _M. extensor ilio-tibialis lateralis_, by a separate and independent tendon in _G. americana_, and apparently by a continuation of the main tendon in _G. canadensis_. In _Balearica_, and apparently in _Grus_, the inserting tendon lies deep to that of _M. extensor ilio-tibialis lateralis_ (in _Aramus_ the two tendons are continuous).

In the Rallidae the muscle is larger than in _Aramus_. The origin in _Rallus_ extends onto the proximal half of the shaft of the femur, and in _Fulica_ it extends nearly to the proximal end of the shaft (in _Aramus_ it is restricted to the distal half). In both rallids the inserting tendon lies deep to the aponeurosis of _M. extensor ilio-tibialis lateralis_, and

the connection to it is very small (in _Aramus_ the edges of the two tendons adjoin and are extensively fused to each other). In neither rallid does the muscle connect to the patellar tendon.

Summary. This muscle in the rallids is considerably larger than in _Aramus_ and the gruids, and its origin is more extensive. In the rallids the muscle has no connection to the patellar tendon, but in _Aramus_ and the gruids such a connection is present. Only in _Aramus_ does the tendon adjoin the posterior edge of the aponeurosis of _M. extensor iliotibialis lateralis_. In Rallidae and Gruidae it lies deep to that aponeurosis.

130. _M. obturator externus_

Very small muscle composed of two mostly separate, flattened heads; upper head thicker and larger and lies dorsal to lower head. Located on posterior aspect of proximal end of femur. Attaches to ischium, to pubis, to _M. obturator internus_, and to femur.

Lies deep to _M. piriformis_ and _M. flexor ischio-femoralis_ and partly deep to tendon of _M. obturator internus_. Upper head dorsal, and lower head ventral, to distal end of belly of _M. obturator internus_. Lower head lies just dorsal to portion of origin of _M. adductor profundus_. Distal tendon superficial to tendon of _M. obturator internus_.

Origin. Upper head arises mostly fleshily from lateral face of triangular area of ischium, just dorsal to obturator foramen; dorsal corner of area of origin lies between

ilio-ischiatic fenestra and acetabulum. Lower head arises by aponeurosis from dorsal edge of portion of pubis forming obturator foramen.

Insertion. Distal portion of lower head inserts fleshily on tendon of M. obturator internus. Two heads fuse by aponeurosis over latter tendon and insert anterior to it on narrow line in posterior region of lateral face of proximal end of femur, about 2 mm dorsal to insertion of M. piriformis. Insertion completely deep to latter muscle.

Action. Rotates external region of leg posteriad.

Comparisons. In the Gruidae the muscle in G. canadensis is sometimes undivided, but in the other two cranes (and Aramus) it is composed of two heads. In G. americana the lower head is larger, but in Balearica (and Aramus) the upper head is definitely larger. In Balearica (and Aramus) the lower head arises from the entire ventral border of the obturator foramen, but in Grus it arises only from the anterior portion of the ventral border. In Balearica (and Aramus) the muscle inserts on the lateral face of the femur, but in Grus it attaches to the obturator ridge. In the cranes the insertion on the femur is partly fleshy (completely tendinous in Aramus), but only in G. americana is there a fleshy insertion deep to the insertion of M. obturator internus. The muscle in Balearica (and Aramus) is more effective in rotating the femur, but in Grus it is more effective in drawing it posteriad, because of the more posterior location of the insertion (see Fisher, 1946).

In the Rallidae the lower head is larger and more independent of _M_. _obturator internus_ than is the upper (in _Aramus_ the upper head is larger and more independent). The lower head is comparatively quite large in _Fulica_. In both rallids the two heads are elongate (more sheet-like in _Aramus_).

Summary. The upper head is the larger in the _Aramus_ and _Balearica_, but in _G_. _americana_ and Rallidae the lower head is larger (unknown for _G_. _canadensis_). The insertion in _Aramus_, _Balearica_, and the two rallids is on the lateral face of the proximal end of the femur, but in _Grus_ it is on the obturator ridge. The lateral insertion probably allows for more rotation of the femur, and the more posterior insertion in _Grus_ probably is better suited for drawing the femur posteriad.

131. _M_. _obturator internus_

Muscle with medium-sized, flat and triangular belly. Fibers converge bipinnately in ventral region of belly to give rise to strong tendon at anterior end. Located mainly on inside of pelvis, but tendon and small anterodorsal portion of belly extend through obturator foramen and emerge posterior to hip joint. Attaches to pelvis, to _M_. _obturator externus_, and to femur.

Posterior corner of belly lies on deep side of portion of ischio-pubic ligament from which _M_. _flexor cruris medialis_ arises. Distal end of belly lies between two heads of _M_. _obturator externus_, and tendon lies partly superficial and partly deep to that muscle.

Origin. Arises mostly fleshily from large area of inside of pelvis, including all but most dorsomedial edge of renal bar of ilium and inner surface of ischium posterior to obturator foramen, as well as flange along dorsal edge of inner side of entire length of pubis, and apparently from ischio-pubic ligament as well. Origin contacts origin of *M. lateralis coccygis*.

Insertion. Strong tendon forms in ventral region of belly and passes through obturator foramen to insert strongly onto small scar on posterior region of lateral face of proximal end of femur, just posterior and deep to insertion of *M. obturator externus* and partly fused to it. Lower head of *M. obturator externus* inserts on tendon.

Action. Rotates external portion of leg posteriad.

Comparisons. In the Gruidae the muscle in *Balearica* (and *Aramus*) arises partly from a dorsal flange along the inside of the pubis and apparently from the ischio-pubic ligament. In *G. americana*, and apparently in *G. canadensis*, the muscle does not arise from the pubis; however, Hudson (1937) listed this muscle as typical in the latter species, and his typical condition (p. 26) includes origin from the pubis, although not from the ischio-pubic ligament. In *Balearica* (and *Aramus*), but not in *Grus*, some fleshy fibers emerge to the outside of the obturator foramen. The inserting tendon in *Balearica* arises by convergence of dorsal and ventral tendinous areas of the belly, but in *Grus* it arises from one central area (in *Aramus* it arises from a single area near the ventral edge of the belly). In *Balearica* (and *Aramus*) the

insertion is on the lateral face of the femur, but in *Grus* it is on the obturator ridge.

In the Rallidae this muscle is composed of two distinct heads, one similar to and corresponding to the single belly of *Aramus*, and another large and very thick head arising from the ventral surface of the posterolateral portion of the ilium. The latter head fills the large excavation in the posterior region of the renal depression and is separated from the more ventral head by the renal bar of the ilium (the latter head is completely absent in *Aramus*). This second head has been described for *Fulica* and *Porzana carolina* by Hudson (1937). The more medial head arises from a similar area of the ilium, ischium, and pubis in both rallids (the area corresponds well to the origin of the single belly in *Aramus*). In both rallids a small dorsomedial portion arises from the ventral surfaces of the last fused caudal vertebrae (this origin is absent in *Aramus*). The origin of this head has more tendinous fibers in *Fulica* than in *Rallus* (or *Aramus*). In both rallids the medial head gives rise to two tendons (only one in *Aramus*), which fuse with a tendon from the lateral head before inserting on the femur.

Summary. In *Aramus* and Gruidae this muscle has only one head, but the Rallidae differ significantly in having an additional head arising from the pelvis inside the posterior excavation of the renal depression. The muscle arises from the pubis in *Aramus*, *Balearica*, and Rallidae, but not in *Grus*. In Rallidae only, some of the origin is from caudal vertebrae.

The proximal portion of the inserting tendon is varied in Gruidae, being single in Grus and Aramus, and partly doubled in Balearica. Two tendons also are formed in the corresponding portion of the muscle in Rallidae, and an additional third tendon forms within the dorsal head. In all three families all tendons combine to form a single inserting tendon. The insertion agrees in Aramus, Balearica, and the Rallidae, in being on the lateral face of the proximal end of the femur. In Grus the insertion is on the obturator ridge. Because of the more posterior location, the muscle in Grus is probably less effective as a rotator of the femur than it is in the other genera.

132. M. psoas

Very small band of muscle. Lies just anteroventral to acetabulum. Attaches to ilium and to femur.

Deep to M. iliacus and M. vastus medialis. Superficial in lateral view to a proximal portion of M. ambiens.

Origin. Arises fleshily from small area of ilium, just ventral to posterior end of origin of M. iliacus and about 6 mm anteroventral to acetabulum.

Insertion. Inserts fleshily on triangular area of medial face of femur, about 6 mm distal to head. Bordered posteriorly by posterior intermuscular line and distally by origin of M. femoritibialis internus.

Action. Flexes femur forward, adducts it, and may rotate its anterior edge outward. Fisher (1946) mentioned rotation in opposite direction as part of action.

Comparisons. In the Gruidae the muscle in Balearica (and Aramus) is rounded, but it is flattened in Grus. In Balearica and G. canadensis (and Aramus) the origin is from a triangular area at the ventral edge of the ilium, but in G. americana this attachment apparently is, if like that of Coragyps, (Fisher, 1946) on a very small and narrow line, well dorsal to the ventral edge. In Balearica and G. canadensis (and Aramus) the insertion is on the medial face of the femur, but on the posteromedial face in G. americana.

In the Rallidae the muscle in Rallus is thicker than in Aramus, and still thicker in Fulica. In both rallids the insertion is on the posteromedial face of the femur (in Aramus it is on the medial face of the femur).

Summary. The muscle is thicker in Rallidae than in Aramus or Gruidae. The insertion is on the posteromedial face of the femur in G. americana and Rallidae, but in the other cranes and Aramus it is on the medial face. The insertion in G. americana is located somewhat posterior to that of the other two cranes and the non-gruids.

133. M. gastrocnemius

Large muscle composed of three heads that converge to form long tendon of Achilles. Belly of external head medium-sized, very thick in middle but attenuate at each end, with distal end continuing as flat and narrow ossified tendon. Internal head similar in size and appearance to external head, but wider and thinner and not so attenuate at proximal end. Medial head quite small and short, but similarly

attenuate and tendinous at both ends. External head lies on posterolateral region of shank, internal head located toward anterior edge of inner surface of shank, and medial head located in posterior portion of upper fourth of shank. This complex attaches to femur, to *M. flexor perforans et perforatus digiti* II, to guide loop, to *M. flexor cruris lateralis*, to *M. flexor cruris medius*, and to tarsometatarsus.

The condition of the muscle as illustrated by Mitchell (1901) for *Aramus scolopaceus* (*A. guarauna*) is the same as that found in this study.

External head deep at proximal end to *M. femoritibialis externus*. Same head lies lateral to and in contact with medial head but partially separated from it by distal end of *M. extensor ilio-fibularis*, running between two heads. Connected to *M. peroneus longus* by strong superficial fascia. External head partly superficial to belly of *M. flexor perforans et perforatus digiti* II, to *M. flexor perforatus digiti* IV, and to *M. flexor perforatus digiti* IV. Internal head lies along inner side of medial head and *M. tibialis anterior*. Superficial to distal ends of *M. extensor ilio-tibialis anterior*, *M. ambiens*, and *M. femoritibialis externus*. Superficial and connected to distal ends of *M. flexor cruris lateralis* and *M. flexor cruris medialis.*

Medial head lies between *M. flexor perforatus digiti* IV laterally, and *M. flexor cruris lateralis* and internal head of *M. gastrocnemius* medially.

Origin. External head arises tendinously, in common with distal arm of guide loop of _M_. _extensor_ _ilio-fibularis_, from well defined oval facet on posterolateral corner of femur, just proximal to fibular condyle. Origin connects indirectly, by vinculum of guide loop, to _M_. _flexor_ _perforans_ _et_ _perforatus_ _digiti_ II. Deep side of proximal end has ossified tendon beginning near origin and extending for about 20 mm.

Internal head originates mostly fleshily from superficial surface of patellar tendon, from tendon of _M_. _femoritibialis_ externus, from medial surface of proximal end of _M_. _peroneus_ _longus_, and by mixed origin from all but distal corner of inner face of inner cnemial crest of tibiotarsus.

Medial head arises by strong, strap-like tendon from distal region of popliteal area of femur, just proximal to internal condyle and in contact with origin of proximal accessory head of _M_. _flexor_ _cruris_ _lateralis_. Tendon of origin partly connected to latter head and also to _M_. _flexor_ _perforatus_ _digiti_ IV.

Insertion. Strap-like, ossified tendon of insertion forms in distal lalf of shank; main portion contributed by wide, ossified tendon arising in distal end of belly of internal head. This tendon narrows and receives, by flexible tendinous attachment three-quarters way out tibiotarsus, the ossified tendon of external head. Medial head forms tendon at distal end and fuses to belly of internal head, just distal to point of fusion of distal accessory head of _M_. _flexor_

cruris lateralis. Single tendon then passes distad down posterior edge of tibiotarsus, loses ossification in distal seventh of shank, passes over intratarsal joint as wide pad. Inserts strongly onto whole posterior face of inner calcaneal ridge and on outer edge of outer ridge of hypotarsus, and forms strong sheet that attaches to inner and outer surfaces of full length of shaft of tarsometatarsus. Strong superficial sheet of connective tissue binds tendon to intratarsal joint and merges with it to contribute to sheet of insertion distal to hypotarsus. This sheet forms sheath enclosing all other tendons passing along posterior surface of intratarsal joint and tarsometatarsus.

Action. Extends tarsus.

Comparisons. In the Gruidae, *Balearica* has extensive fleshy and tendinous connection of the distal ends of the bellies of all three heads of origin. In *Grus* the external head fuses fleshily with the medial head, but the medial head connects to the internal head only by its distal tendon(in *Aramus* there is no fleshy fusion of the bellies, but the tendon of the medial head connects to the internal head as in *Grus*). In one specimen only of *G. canadensis* Berger (1956a) found an "accessory medial head," arising from the medial condyle and attaching to the external head. In *Balearica* (and *Aramus*) the external head arises from a scar proximal to the fibular condyle, but in *Grus* it arises from the flexor attachment. In *Balearica* and *G. canadensis* (and *Aramus*), but not in *G. americana*, the external head arises partly from the

guide loop of _M_. _extensor_ _ilio-fibularis_. In _Balearica_ (and _Aramus_) a short ossified tendon is associated with the origin of the external head, but this ossification is apparently absent in _Grus_. In _Balearica_, but not in _Grus_, the external head arises partly from _M_. _flexor_ _perforans_ _et_ _perforatus_ _digiti_ II (in _Aramus_ there is some indirect connection). In _Balearica_ the internal head has conspicuous fleshy origin from the distal end of the belly of _M_. _extensor_ _ilio-tibialis_ _anterior_. This origin in _Grus_ (and _Aramus_) is distal to that belly, and arises from the patellar tendon only. In the three cranes the medial head is not connected to _M_. _flexor_ _perforatus_ _digiti_ IV (in _Aramus_ the tendon of origin is fused to that muscle). In _Balearica_ (and _Aramus_) the main tendon inserts strongly on the inner calcaneal ridges, as well as on the shaft of the tarsometatarsus. In _Grus_ it also connects to the calcaneal ridges, but only weakly.

In the Rallidae the medial head is apparently absent, although Hudson (1937) seems to have found it in _Fulica_. The condition of _M_. _gastrocnemius_ found in the rallids is the same as that illustrated by Mitchell (1901) for _Rallus_ _longirostris_; his drawing shows no medial head, although it could be hidden. The medial head may be combined with the distal accessory head of _M_. _flexor_ _cruris_ _lateralis_, which has very similar attachments, but the latter head in the rallids appears similar to that of the non-rallids, in which the medial head is distinct. In _Fulica_ the external, and especially the internal, heads are bulkier than in _Rallus_ (or _Aramus_). In _Fulica_, but not _Rallus_ (or _Aramus_), the internal

has a shallow, lengthwise division on the superficial side of the belly. The external head arises by a narrow tendon in both rallids (arises partly fleshily in _Aramus_). In _Rallus_ the tendon connects to the guide loop only at the point of origin, but in _Fulica_ (and _Aramus_) the two are intimately connected. In neither rallid is there connection to _M. flexor perforans et perforatus digiti_ II (indirect connection in _Aramus_). In both _Rallus_ and _Fulica_ the internal head arises from a wider area of the tibiotarsus and has conspicuous fleshy origin from the distal end of the belly of _M. extensor ilio-tibialis anterior_ (in _Aramus_ the origin from the tibiotarsus is smaller, and it arises from the patellar tendon distal to the latter muscle). The connection to _M. flexor cruris medialis_ is more extensive in both rallids than in _Aramus_. In neither rallid does the origin of the medial head connect to _M. flexor perforatus digiti_ IV (connects in _Aramus_). In _Rallus_ no ossification is present in the tendons, but in _Fulica_ the main tendon is ossified (in _Aramus_ the main tendon and the tendons of origin and insertion of the external head are all ossified).

Summary. _Aramus_ agrees with Gruidae in having three heads to this muscle; in Rallidae only two heads are present. In Gruidae there is a variable amount of fusion of the bellies, and in _Balearica_ all three are extensively connected; in _Aramus_ and Rallidae the heads connect only by their tendons. In _G. canadensis_ only, the medial head may be doubled. In _Fulica_ the external and internal heads are larger than

those of Rallus or the non-rallines. Ossification of the tendons is apparently most extensive in Aramus and Balearica, somewhat less in Grus, still less in Fulica, and completely absent in Rallus. Various other minor variations are found among the genera.

134. M. peroneus longus

Wide and thickly sheet-like muscle with belly oval-shaped in lateral view. Long tendon forms superficially and becomes free at distal end of belly, in middle of shank. Located mainly on anterolateral surface of shank. Attaches to patellar tendon, to internal head of M. gastrocnemius, to M. flexor perforatus digiti IV, M. flexor perforans et perforatus digiti III, to M. flexor perforans et perforatus digiti II, to M. tibialis anterior, to tibiotarsus, to flexor tendons, and to M. flexor perforatus digiti III.

Small portion of proximal end deep to internal head of M. gastrocnemius. Medial edge of belly adjoins and connects to internal head of M. gastrocnemius. Connected to M. flexor perforatus digiti IV and to external head of M. gastrocnemius by superficial fascia, and on side of shank belly fuses with belly of M. flexor perforans et perforatus digiti II. Superficial to most of belly of M. tibialis anterior, and deep side of anterior end connected extensively to it.

Origin. Arises fleshily from underlying M. tibialis anterior and from adjacent muscles, but originates mainly from tibiotarsus; arises partly in common with M. flexor perforans et perforatus digiti II, by mixed fleshy and tendinous fibers,

from lateral edge and lateral border of anterior face of outer cnemial crest and by two ossified tendons arising from distal extension of this crest. Arises also by mixed fibers from definite scar along anterior and proximal border of lateral face of inner cnemial crest. Arises in common with _M. digitorum longus_ from ossified, tendinous extension of distal edge of inner cnemial crest, and origin continues to middle of shaft on intermuscular line.

Insertion. Strong, ossified tendon forms from dissected, fan-shaped area on superficial side of distal two-thirds of belly. Tendon leaves distal end of belly in middle of shank and passes directly to outer side of intratarsal joint, where strong vinculum arises and connects tendon to flexor tendons and tibial cartilage on posterior side of joint. Tendon continues distad, but now unossified and only half as wide, through sheath on lateral face of joint. Inserts strongly on lateral edge of ossified tendon of _M. flexor perforatus digiti_ III just within proximal fourth of tarsus.

Action. Extends tarsus and flexes digit III.

Comparisons. In the Gruidae the fibers of this muscle in _Balearica_ (and _Aramus_) are more nearly parallel or radiating than truly bipinnate as described for _G. americana_. In _Balearica_ (and _Aramus_) there is no origin from the portion of the tibiotarsus between the two cnemial crests, but this portion of the muscle arises from the patellar tendon; in Grus there is no mention of origin from this tendon, but the muscle arises from the region between the two crests. In

G. americana the muscle arises "from the external face of the inner cnemial crest" (Fisher and Goodman, 1955, p. 93); this origin is apparently similar in G. canadensis, but in Balearica (and Aramus) it is from only the outer border of this face of the crest. In G. canadensis the insertion on M. flexor perforatus digiti III is well within the proximal fourth of the tarsus, but it is at least one-fourth of the way out the tarsometatarsus in the other two cranes (and Aramus).

In the Rallidae the origin from the inner cnemial crest is only from the anterior edge (in Aramus it arises from the outer border of the lateral face of the crest). The belly extends slightly beyond the middle of the shank (ends at middle in Aramus), and the tendon has no ossification (present in Aramus). The vinculum to the flexor tendons is the same, but the distal insertion, on M. flexor perforatus digiti III, is about half way down the tarsus (in Aramus it is just beyond the proximal fourth).

Summary. In Aramus and Gruidae the belly is slightly shorter than in Rallidae. Only in Grus is there origin from the region of the tibiotarsus between the two cnemial crests. In Aramus, Balearica and Rallidae this origin is from the patellar tendon. In Grus the muscle arises from the lateral face of the inner cnemial crest, from the outer border of this face in Balearica and Aramus, and only from the anterior edge of the crest in Rallidae. Aramus agrees with the gruids in having ossification of the tendon, but ossification is lacking in the Rallidae. IThe insertion on M. flexor

perforatus *digiti* III is most distal in Rallidae, intermediate in *Aramus*, *Balearica*, and *G*. *americana*, and most proximal in *G*. *canadensis*.

135. *M*. *tibialis* *anterior*

Medium-sized, rounded muscle divided proximally into distinctly bipinnate bellies (anterior head and femoral head) that fuse at their distal ends. Common belly tapers to narrow tendon in middle of shank. Runs along anterolateral face of length of tibiotarsus, crossing to anterior face of proximal half of tarsus. Attaches to femur, to *M*. *peroneus* *longus*, to patellar tendon, to tibiotarsus, and to tarsometatarsus.

Belly completely deep to, partially enclosed by, and extensively fused to belly of *M*. *peroneus* *longus*. Partly deep to *M*. *flexor* *perforans* *et* *perforatus* *digiti* III. Lies completely superficial to belly of *M*. *extensor* *digitorum* *longus* and lies anterior and partially superficial to belly of *M*. *peroneus* *brevis*.

Origin. Larger anterior head arises partly from patellar tendon, but mainly from tibiotarsus. Arises mostly fleshily from anterior face of outer cnemial crest, similarly from all but outer edge of inner cnemial crest. Arises in common with *M*. *peroneus* *longus*, from tendinous sheet attaching to intermuscular line and forming distal continuation of inner crest and also from narrow line connecting proximal ends of inner and outer crests. Extensive fleshy connection to underside of *M*. *peroneus* *longus* may also be considered as origin. Femoral head arises strongly by small tendon from depressed

scar on distal aspect of external condyle, just lateral to rotular groove.

Insertion. Two bellies fuse distally to form narrow, band-like, ossified tendon that continues along anterior face of shank, passes under strong ligamentous bridge, and across anterolateral area of intratarsal joint. Just past joint, tendon bifurcates, and each branch inserts on small tubercle on anterior face of extreme proximal end of shaft of tarsometatarsus. Very minute tendon continues distad from more lateral branch and inserts on anterior face of middle of tarsometatarsus.

Action. Flexes tarsus.

Comparisons. In the Gruidae the anterior head in *Balearica* (and *Aramus*) arises partly from large areas of both cnemial crests and from the patellar tendon. In *Grus* the origin of this head is restricted to the portion of the tibiotarsus between the two crests, but it sometimes arises also from the head of the fibula. In *G. americana* no division of the inserting tendon is mentioned, but in the other two cranes (and *Aramus*) the tendon bifurcates at the distal end. The minute tendon of *Aramus*, extending distad from the main insertion, seems to be absent in the cranes.

In the Rallidae the muscle in *Fulica* is thicker than in *Rallus* (or *Aramus*). In both rallids the anterior head arises partly in common with *M. flexor perforans et perforatus digiti* II (not in common with this muscle in *Aramus*). In both rallids the portion of this head originating from the

inner cnemial crest arises only from the outer edge of the lateral face (in Aramus it arises from all but the outer edge). The inserting tendon has no ossification in Rallus, but in Fulica (and Aramus) it is strongly ossified. In Rallus (and Aramus) the tendon bifurcates at the insertion, but in Fulica it does not divide. In both rallids (as in Aramus) a minute tendon extends distad from the lateral region of the main insertion, but in the rallids it is larger and inserts about two-thirds of the way down the tarsometatarsus (about half way down in Aramus).

Summary. This muscle is somewhat larger in Fulica than in Rallus and the non-rallines. In Grus alone, the anterior head does not arise from the cnemial crests, and only in Rallidae does this head arise partly in common with M. flexor perforans et perforatus digiti II. In Rallus alone, the inserting tendon is unossified. The distal end of the tendon bifurcates in Aramus, Balearica, G. canadensis, and Rallus but does not in G. americana and Fulica. Aramus agrees with Rallidae in having a minute distal tendon not present in Gruidae.

136. M. flexor perforans et perforatus digiti II

Rather small, somewhat bipinnate muscle; belly indistinct proximally because of fusion to other muscles. Distal half of belly very thin; ossified tendon emerges along posterior edge of distal two-thirds of belly and from aponeurotic area near distal end. Located on posterolateral side of

thigh. Attaches to *M. gastrocnemius*, to *M. peroneus longus*, to *M. flexor perforatus digiti* IV, to *M. flexor perforans et perforatus digiti* III, to vinculum of guide loop, to fibula, and to digit II.

Posterior edge of belly deep to external head of *M. gastrocnemius* and partly connected to it anteriorly; proximal end deep to *M. femoritibialis externus*. Lies adjacent to and fused to posterior edge of *M. peroneus longus*. Partly superficial to and connected to *M. flexor perforatus digiti* IV and *M. flexor perforans et perforatus digiti* III.

Origin. Arises from flexor attachment at base of external condyle of femur, continuous with external head of *M. gastrocnemius* and with *M. peroneus longus*, and indirectly connected with patellar tendon; underside of origin intimately connected to origin of *M. flexor perforans et perforatus digiti* III and with vinculum from guide loop of *M. extensor ilio-fibularis*. A few weak tendinous fibers attach to lateral face of shaft of fibula.

Insertion. Ossified tendon forms on superficial surface, along posterior edge of distal two-thirds of belly, and passes along posterior edge of shank under tendon of *M. gastrocnemius*. Loses ossification and passes over posteromedial regions of intratarsal joint and hypotarsus, partially deep and partially medial to tendon of *M. tibialis anterior*. Emerges, becomes ossified again, and follows posterior edge of tarsus, still beneath tendon of *M. gastrocnemius*. At level of base of first digit tendon becomes

thick and passes beneath tendon of M. flexor perforatus digiti II and then penetrates it. Tendon then passes distad on digit II and inserts on phalanx 1, along medial edge of distal three fourths and on lateral corner of distal end. Also inserts on adjacent corners of proximal end of phalanx 2, at which point tendon of M. flexor digitorum longus penetrates tendon.

Action. Flexes digit II and extends tarsus.

Comparisons. In the Gruidae the belly in G. americana has a complex bipinnate structure, but in G. canadensis the bipinnate structure is simpler and sometimes absent, or as in Balearica (and Aramus), it is poorly developed. In Balearica (and Aramus), but not in Grus, the muscle connects to the guide loop. In Grus part of the origin is from the patellar tendon and outer cnemial crest, but in Balearica (and Aramus) these origins are absent. In Balearica ossified tendons from the posterior end of the belly converge to form the main tendon (a portion of this area is collagenous aponeurosis in Aramus). In Grus the configuration of this area is not discussed. In Balearica and G. canadensis (and Aramus) ossification in the tendon is well developed along the shaft and the tarsus, but this is not mentioned for G. americana. Sometimes in G. canadensis the tendon fuses with the tendon of M. flexor perforatus digiti II, but the two are not found connected in the other two cranes(or Aramus). In Balearica (and Aramus) the perforation by M. flexor digitorum longus is nearly equal, and the tendon inserts on most of the length of

phalanx 1 and on the proximal end of phalanx 2. In _Grus_ the latter perforation is unequal, the medial side of the tendon is branched, and the main insertion is on the claw of the digit.

In the Rallidae the belly in _Fulica_ is much wider and more complexly bipinnate than in _Rallus_ (or _Aramus_). In both rallids most of the connection to _M. flexor perforatus digiti_ IV is weak (in _Aramus_ this fusion is very intimate). In _Rallus_ there is no origin in common with the latter muscle, but in _Fulica_ there is a small portion in common with it (larger portion in _Aramus_). In neither rallid is there direct connection to either _M. gastrocnemius_ or the guide loop (both connections are present in _Aramus_). In _Fulica_ most of the origin from the femur is fleshy, and some of it is fleshy in _Rallus_ (in _Aramus_ this origin is entirely tendinous). In neither rallid is there ossification of the tendon (it is extensively ossified in _Aramus_). The distal region of the tendon is similar in both rallids (and _Aramus_).

Summary. The belly is wider in _Fulica_ than in _Rallus_ or the non-rallids. In _G. americana_ and _Fulica_ the belly has a more complex arrangement of fibers than in the other genera. In _Aramus_, _Balearica_, and the two rallids the muscle has no origin from the patellar tendon or the tibiotarsus, but both these origins are present in _Grus_. In _Aramus_ and _Balearica_ only, the muscle connects to the guide loop of _M. extensor ilio-fibularis_. The inserting tendon has two extensive regions of ossification in _Aramus_, _Balearica_, and _G._

canadensis (not mentioned for *G. americana*), but no ossification is present in Rallidae. In *Grus* only, the main insertion is on the claw.

137. *M. flexor perforans et perforatus digiti* III

Small muscle with flat, spatulate, and strongly bipinnate belly; inserting tendon long. Belly lies along anterolateral face of proximal third of shank. Attaches to patellar tendon, to tibiotarsus, to *M. peroneus longus*, to *M. flexor perforans et perforatus digiti* II, to vinculum of guide loop, loosely to tendon of *M. ambiens*, and indirectly to head of fibula.

Belly deep to *M. peroneus longus*, to *M. flexor perforans et perforatus digiti* II, and to *M. flexor perforatus digiti* IV. Superficial to portions of *M. tibialis anterior*, *M. flexor perforatus digiti* II, and to tendon of *M. ambiens*.

Origin. Complex, but mainly from patellar tendon and small posterolateral area of outer cnemial crest of tibiotarsus. Other connections listed above might be considered as minor portions of origin.

Insertion. Tendon forms along middle of bipinnate belly, becomes ossified at distal end of belly, and passes along shank. Passes intratarsal joint in unossified condition and continues along tarsometatarsus as ossified tendon. At level of base of first digit tendon connects by vinculum to tendon of *M. flexor perforatus digiti* III and then passes deep to it. Tendon thickens, perforates latter tendon near center of phalanx 1 of digit III, and is perforated by tendon of *M.*

flexor digitorum longus near center of phalanx 2. Tendon divides at latter perforation, and resulting branches insert on either edge of full length of phalanx 2.

Action. Flexes digit III and extends tarsus.

Comparisons. In the Gruidae the origin from the shaft of the fibula is absent in *Balearica* (and *Aramus*), but present in *Grus*. In *Balearica* (and *Aramus*) the inserting tendon is ossified along the shank and again along the tarsus, but for *Grus*, ossification is mentioned only along the shank, and for *G. americana* only. In *Balearica* and *G. canadensis* (and *Aramus*) the vinculum connecting the tendon to that of *M. flexor perforatus digiti* III is present. In *Balearica* (and *Aramus*) the tendon is perforated by the tendon of *M. flexor digitorum longus* at phalanx 2. In *G. americana*, and apparently in *G. canadensis*, the vinculum is lacking, and the perforation is opposite phalanx 1. In *Balearica* (and *Aramus*) the tendon inserts along the length of phalanx 2, but in *Grus* the insertion is distal to this phalanx.

In the Rallidae, but especially in *Fulica*, the belly is thicker thanin *Aramus*, and in both rallids it extends along the proximal half of the shank (proximal third in *Aramus*). In both *Rallus* and *Fulica* the belly is more extensively connected to the belly of *M. flexor perforans et perforatus digiti* II, especially along the anterior edge. In *Rallus* the inserting tendon lacks ossification, but in *Fulica* it is ossified on both shank and tarsus (as in *Aramus*). In *Rallus* the vinculum is quite long, arising near the base of digit I but connecting to *M. flexor perforatus digiti* III at about

one-third of the way proximad on the tarsus. In *Fulica* the vinculum is considerably shorter and lies within the distal fourth of the tarsus (lies within the distal fifth in *Aramus*). In *Rallus* the tendon perforates the tendon of *M. flexor perforatus digiti* III near the base of phalanx 1 and is perforated near the base of phalanx 2. In *Fulica* (and *Aramus*) these points are near the center of phalanges 1 and 2, respectively.

Summary. The origin from the shaft of the fibula is present only in *Grus*. The belly is thicker in *Rallus* than in *Aramus* or the gruids, and in *Fulica* it is very much thicker. The belly is longer in Rallidae than in *Aramus* or Gruidae. In the rallids the belly is more extensively connected to *M. flexor perforans et perforatus digiti* II than in the other two families. The inserting tendon is ossified on both shank and tarsus in *Aramus*, *Balearica* (undetermined for *G. canadensis* and for the tarsus of *G. americana*), and *Fulica*, but ossification is entirely lacking in *Rallus*. The vinculum is lacking only in *G. americana*. In *Rallus* it is considerably longer than in *Fulica* and the other species included in this study. In *G. americana*, and apparently in *G. canadensis*, the inserting tendon is perforated along phalanx 1, but in *Balearica* and in the other two families this perforation is along phalanx 2. The insertion is on at least most of the length of phalanx 2 in each genus studied except *Grus*, in which the insertion is located more distally.

138. M. flexor perforatus digiti IV

Rather small muscle with belly composed of wide and flattened lateral head and small, narrow and bipinnate medial head. Belly extends slightly beyond proximal half of thigh; inserting tendon long. Lies within posterolateral region of thigh. Attaches to M. flexor perforans et perforatus digiti II, to M. flexor perforatus digiti III, to M. flexor perforatus digiti II, to M. ambiens, and to femur.

Belly partly deep to external head of M. gastrocnemius and to M. flexor perforans et perforatus digiti II. Proximal end of medial head deep to M. extensor ilio-fibularis and to M. extensor ilio-tibialis lateralis. Lies partly superficial to M. flexor perforatus digiti III and M. flexor perforatus digiti II.

Origin. Small, lateral head arises partly by small, fleshy fasciculus from region of fusion of proximal ends of lateral head of M. flexor perforatus digiti III and M. flexor perforatus digiti II, at point where latter muscles fuse with distal end of inserting tendon of M. ambiens. Proximal end of lateral head arises by aponeurosis from belly of lateral head of M. flexor perforatus digiti III. Medial head has mixed origin, mainly from small portion of popliteal area of femur, but strong attachment to underlying medial head of M. flexor perforatus digiti III may also be considered as origin.

Insertion. Two heads fuse in distal third of belly, and ossified tendon arises along posterior edge of belly and extends to intratarsal joint. Tendon crosses joint in unossified condition, just superficial to tendon of M. flexor

perforatus digiti III, and passes along tarsus as ossified tendon. At base of digit IV present tendon forms sheath around tendon of M. flexor digitorum longus. At distal border of latter sheath tendon divides into four branches that attach to digit IV. One very short, medial branch inserts just proximal to center of ventromedial edge of phalanx 1. Another short branch comes off lateral edge of tendon and inserts near distal end of ventrolateral edge of phalanx 1. Main portion of tendon continues distad to insert on distal half of ventrolateral edge of phalanx 2. Another long, narrow tendon arises from deep side of main tendon at base of digit IV and continues distad to insert on distal end of ventromedial edge of phalanx 3. Tendon of M. flexor digitorum longus perforates present tendon by passing between latter two branches at level of phalanx 2.

Action. Flexes digit IV and extends tarsus.

Comparisons. In the Gruidae the belly covers only the proximal two-fifths of the shank (covers proximal half in Aramus). In Balearica the lateral head of origin arises mainly from the patellar tendon but also partly from the guide loop and from M. flexor perforans et perforatus digiti III. In Grus this origin is from the femur and the guide loop (in Aramus the proximal end of this head does not reach the knee but arises entirely from M. flexor perforatus digiti III). In Balearica (and Aramus) the small fasciculus of the lateral head arises from common tendon of M. ambiens, M. flexor perforatus digiti III, and M. flexor perforatus digiti II and

has only indirect connection to the fibula; in *Grus* this fasciculus arises directly from the head of the fibula. In the cranes (and *Aramus*) the main origin of the medial head is largely similar, but *Balearica* is distinct in having a small tendinous origin from the patellar tendon, and *Grus* is distinct in having fusion at this point with *M. flexor hallucis longus* (neither is present in *Aramus*). In *Balearica* (and *Aramus*) the tendon is perforated by *M. flexor digitorum longus* along phalanx 2, but this perforation occurs along phalanx 1 in *Grus*. In *Balearica* (and *Aramus*) the short, medial tendon inserts at the middle of the length of phalanx 1, but in *Grus* it inserts on the distal end of that phalanx. In *Balearica* (and *Aramus*) the two distal insertions are effected by two long tendons that separate near the base of digit IV. In *Grus* these insertions are apparently effected by a more distal bifurcation of the main tendon and are located slightly more distally than in *Balearica* (or *Aramus*).

In the Rallidae, but especially in *Fulica*, the muscle is bulkier than in *Aramus* and extends slightly farther distad on the shank. In *Rallus* the main origin of the lateral head connects more directly, and much more directly in *Fulica*, to the patellar tendon than in *Aramus*. In *Fulica* only, there is a small connection to the guide loop. In *Rallus* and *Fulica* the small, deep fasciculus (of *Aramus*) is represented by a wide area of fusion of the underside of the lateral head of *M. flexor perforatus digiti* II and *M. flexor perforatus digiti* III. In both rallids the origin of the medial head is

more strongly connected to M. flexor perforatus digiti III than in Aramus. In both rallids the two short branches of the inserting tendon are similar to those of Aramus. In the rallids the long, lateral branch occupies a smaller insertion than in Aramus and is located slightly more proximally in Rallus, slightly more distally in Fulica. In Rallus the long, medial branch inserts on the proximal end of phalanx 2, but in Fulica (and Aramus) it inserts on the distal end of phalanx 3. No ossification of the inserting tendon is found in either rallid (highly ossified in Aramus).

Summary. The length of the belly is greatest in Rallidae, least in Gruidae, and intermediate in Aramus. In Rallidae, expecially Fulica, the muscle is bulkier than in Aramus or Gruidae. The main origin of the lateral head is variable, but it arises directly from the femur in Grus, directly from the patellar tendon in Balearica, indirectly from that tendon in Rallidae, and from M. flexor perforatus digiti III in Aramus. A small fasciculus of the lateral head arises from the fibula in Grus and from M. ambiens and other associated muscles in Balearica and Aramus. In Rallidae this origin is represented only by a large area of fusion to the surrounding muscles. The origin of the medial head is rather constant, but minor variations are found within the Gruidae. The perforation of the inserting tendon and the branches of the tendon vary only slightly among the members of the three families. The inserting tendon is highly ossified in Aramus and Gruidae, but is completely unossified in Rallidae.

139. M. flexor perforatus digiti III

Somewhat small muscle with two bipinnate heads that connect at distal ends; lateral head short and small, posterior head longer and thicker. Bellies lie within posterior portion of proximal half of shank. Lateral head occupies second fourth and posterior head occupies proximal half of shank. Inserting tendon long. Connects to M. flexor perforatus digiti IV, to M. flexor perforatus digiti II, to M. flexor digitorum longus, to M. ambiens, and indirectly to femur and to fibula. Inserting tendon connects to tendon of M. peroneus longus and, by vinculum, to tendon of M. flexor perforans et perforatus digiti III.

Lies mostly deep to M. flexor perforatus digiti IV, but posterior edge lies deep to external head of M. gastrocnemius. Lies lateral to medial head of latter muscle and to portions of M. flexor perforatus digiti II.

Origin. Small, lateral head arises from inserting tendon of M. ambiens and by tendon from head of fibula, partly in common with M. flexor perforatus digiti II and partly in common with small fasciculus of lateral head of M. flexor perforatus digiti IV. Larger posterior head is extensively fused with M. flexor perforatus digiti II and with medial head of M. flexor perforatus digiti IV. It arises primarily from these muscles and only indirectly from femur.

Insertion. Lateral head becomes narrow tendon at distal end. This tendon is closely bound, along distal half of shank, to tendon of posterior head and fuses with it near

distal end of tibiotarsus. Ossified tendon forms in distal third of medial head and continues length of shank. Passes intratarsal joint as unossified tendon, just deep to tendon of _M. flexor perforatus digiti_ IV, and continues length of tarsus, again in ossified condition. Just distal to intratarsal joint lateral edge of ossified tendon acts as main insertion for tendon of _M. peroneus longus_. Just proximal to base of digit I tendon connects by vinculum to tendon of _M. flexor perforans et perforatus digiti_ III. At foot tendon becomes superficial to latter tendon but is perforated by it and also by tendon of _M. flexor digitorum longus_, along phalanx 1 of digit III. Tendon divides into two branches at latter perforation. More medial branch attaches to ventromedial edge of most of length of phalanx 1, and lateral branch attaches to ventrolateral edge of proximal end of phalanx 2.

Action. Flexes digit II and extends tarsus.

Comparisons. In the Gruidae the lateral head in _Balearica_ (and _Aramus_) has no fibular attachment, but this attachment is present in _Grus_. In _Balearica_ (and _Aramus_) the posterior head arises mainly from _M. flexor perforatus digiti_ II, although some tendinous fibers may be traced to the femur (fewer of these in _Aramus_). In _Grus_ the main origin of this head is from the femur but it arises also by fascia from the other muscles in the area. In _Balearica_ only, the tendon of the lateral head is ossified, and the fusion of the two tendons is proximal to the distal fifth of the tibiotarsus. This fusion is just proximal to the intratarsal joint in

Grus (and Aramus). In G. americana only, the vinculum to the tendon of M. flexor perforans et perforatus digiti III is lacking. In Balearica (and in Aramus) the medial branch of the tendon inserts on most of the length of phalanx 1, but in Grus it inserts on the distal end. In Balearica the lateral branch inserts on the distal two-thirds of phalanx 1, and in Grus it attaches to the distal end (in Aramus it inserts on the proximal end of phalanx 2).

In the Rallidae both heads in Rallus are similar to those of Aramus, but in Fulica the size of each belly is about twice that of Rallus. In both rallids a small vinculum, near the distal end of the tibiotarsus, loops loosely around the tendon of M. flexor perforatus digiti IV (this vinculum is lacking in Aramus). Ossification is entirely lacking in Rallus and is present only along the tarsus in Fulica (ossified along both shank and tarsus in Aramus). In both rallids the vinculum from the tendon of M. flexor perforans et perforatus digiti III connects farther proximally than in Aramus. In both Rallus and Fulica the two branches of the tendon insert on most of the length of phalanx 1 (in Aramus the lateral branch inserts on the proximal end of phalanx 2).

Summary. In Fulica the size of each belly is double that of Rallus and the non-rallids. The lateral head has a fibular attachment in Grus, but not in Balearica or the non-gruids. Only in Balearica is the tendon of the lateral head ossified, only in Rallidae is ossification entirely absent along the shank, and only in Rallus is it absent along the

tarsus. The rallids differ slightly from Gruidae and *Aramus* in having a small vinculum enclosing the tendon of *M. flexor perforatus digiti* IV. The vinculum connecting to *M. flexor perforans et perforatus digiti* III is lacking only in *G. americana*. The insertions of the branches are slightly variable among the cranes and the limpkin, but are similar within the Rallidae.

140. *M. flexor perforatus digiti* II

Small muscle with flattened, bipinnate belly that divides into superficial and deep heads; inserting tendon long. Located deep within posterolateral aspect of thigh. Connects to *M. flexor perforatus digiti* IV, to *M. flexor perforatus digiti* III, to *M. ambiens*, and to *M. flexor digitorum longus*.

In lateral view lies mostly deep to *M. flexor perforatus digiti* IV and partly deep to *M. flexor perforatus digiti* III. Superficial head divides and passes on either side of insertion of *M. extensor ilio-fibularis*. Lies partly superficial to *M. flexor digitorum longus* and *M. peroneus brevis*.

Origin. Superficial head arises partly by tendon from posterolateral region of head of fibula, in common with other toe flexors in that region; this tendon also serves as portion of origin of *M. flexor perforans et perforatus digiti* III, *M. flexor perforatus digiti* IV, and *M. flexor perforatus digiti* III. Remainder of superficial head arises fleshily from *M. flexor perforatus digiti* IV, *M. flexor perforatus digiti* III, and from *M. flexor digitorum longus.* Deep head

arises fleshily, mainly from tendon of M. ambiens, but also partly from same muscles serving as origin of superficial head.

Insertion. Two heads fuse just beyond proximal third of shank. Ossified tendon forms in distal region of belly and continues down shank, passes unossified across intratarsal joint through separate canal in hypotarsus, and continues as ossified tendon down length of tarsometatarsus. Tendon merges with palmar cartilage and is perforated at base of digit II by tendon of M. flexor perforans et perforatus digiti II. Two short branches form at perforation and insert on either side of proximal end of phalanx 1 of digit II.

Action. Flexes digit II and extends tarsus.

Comparisons. In the Gruidae the two heads in Balearica (and Aramus) are flattened, but in Grus the superficial head is rounded. In Balearica, and probably in Grus, the bellies are narrower than in Aramus. In Balearica (and Aramus) the medial branch of the inserting tendon is strong and only slightly smaller than the lateral branch, but in Grus the medial branch is small and rather insignificant.

In the Rallidae the muscle has a single head (has two separate heads in Aramus), and the medial branch of the inserting tendon is much smaller than the lateral branch (more nearly equal in Aramus). Ossification is entirely absent in both rallids (present in Aramus).

Summary. In Aramus and the gruids the belly is comprised of two heads, but only one head is present in the rallids.

In Balearica and Aramus the medial branch of the inserting tendon is somewhat larger than in Grus or the rallids. Ossification of the inserting tendon is well-developed in Aramus and Gruidae but is absent in Rallidae.

141. M. flexor hallucis longus

Small, slender, and bipinnate belly with long inserting tendon. Lies deep within posterior portion of proximal half of shank. Attaches to M. flexor perforatus digiti II, M. flexor perforatus digiti III, M. flexor perforatus digiti IV, to femur, to M. flexor digitorum longus, and to digit I.

In lateral view lies deep to first three toe flexors named above. Lies superficial to M. flexor digitorum longus.

Origin. Arises from popliteal area of femur in common with M. flexor perforatus digiti II, M. flexor perforatus digiti III, and M. flexor perforatus digiti IV. Above muscles and present muscle are intimately connected in proximal region.

Insertion. Ossified tendon forms in belly and passes unossified across intratarsal joint and through fibrous canal in hypotarsus. Tendon again becomes ossified and passes to point about 1 cm proximal to digit 1, where it gives off vinculum of variable size to that branch of M. flexor digitorum longus passing to digit II. Main tendon passes mediad, perforating tendon of M. flexor hallucis brevis at base of digit I, and extending along digit I to perforate superficial elastic ligament at distal end of phalanx 1 and to insert on palmar face of base of claw.

Comparisons. In the Gruidae small, fleshy origins from the tibiotarsus are present in Grus, but these are absent in Balearica (and Aramus). In G. americana, but not in the other two cranes (or Aramus), the tendon passes through a separate bony canal in the hypotarsus. In Balearica only a weak vinculum passes to the tendon of M. flexor digitorum longus, about two-thirds of way down tarsus. In Grus the tendon sometimes fuses entirely to the tendon of M. flexor digitorum longus and sometimes connects to it only by a vinculum. In the one specimen of Balearica the major part of the tendon fuses with the tendon of M. flexor digitorum longus, but a small branch extends out digit I (in Aramus the tendon connects to the latter by a vinculum, but the major branch extends out digit I). In Balearica (and Aramus) the branch of the tendon passing to digit I perforates the tendon of M. flexor hallucis brevis.

In the Rallidae the belly and the origin are largely similar to those of Aramus, although in Fulica the belly is somewhat larger. In the two rallids the tendon connects, near the middle of the tarsometatarsus, to the tendon of M. flexor digitorum longus by a wide vinculum (in Aramus the connection to this tendon is narrower, farther distal, and less extensive). A small tendon passes from the vinculum to digit I, where it inserts as in Aramus. Ossification of the inserting tendon is lacking in both rallids (present in Aramus).

Summary. Minor variations occur among the cranes, especially in the degree of fusion to the tendon of M. flexor digitorum longus. This fusion may be complete or partial in Grus, but is only partial in Balearica and Aramus. In Rallidae this connection is wider and is located farther proximally. In Aramus, Rallidae, and Balearica a small tendon passes out digit I to perforate other flexor tendon and ligament there and to insert on the claw. A similar tendon is sometimes found in Grus, but it does not perforate. The inserting tendon is well ossified in Aramus, Balearica, and probably Grus, but is not ossified in Rallidae.

142. M. flexor digitorum longus

Rather small but flattened, bipinnate muscle, notched at proximal end by blood vessels and nerves. Belly located on proximal half of posterior face of tarsometatarsus. Attaches to fibula, to tarsometatarsus, to M. flexor hallucis longus, and to digits II, III, and IV.

Lies deep to combined portions of flexor muscles of digits II, III, and IV. Lies lateral to M. plantaris and to medial head of M. gastrocnemius. Inserting tendon of M. extensor ilio-fibularis adjoins lateral edge, and M. popliteus adjoins anterior end. Lies superficial to portion of M. popliteus.

Origin. Arises fleshily from posterior face of proximal two-thirds of fibula, from medial face of proximal two-thirds of tibiotarsus, and from large area beginning at distal edge

of insertion of tarsus, covering entire posterior face of shaft in that region.

Insertion. Ossified inserting tendon runs superficially along nearly entire length of belly but passes intratarsal joint and tibial cartilage in unossified condition. Passes through deepest notch in medial side of hypotarsus, and again becomes ossified along tarsometatarsus. At base of digit I tendon is joined by vinculum from *M. flexor hallucis longus* and immediately divides into three branches. Branch to digit II becomes enclosed within tendon of *M. flexor perforans et perforatus digiti* II, and in that condition passes through perforation in tendon of *M. flexor perforatus digiti* II. Finally perforates latter tendon and gives off elastic branch to phalanx 2 at distal end of digit, and inserts on ventral surface of base of claw. Branch to digit III passes along with tendon of *M. flexor perforans et perforatus digiti* III through perforation in tendon of *M. flexor perforatus digiti* III, perforates former tendon near distal end of phalanx 1, sends elastic branches to distal ends of phalanges 2 and 3, and finally inserts on ventral surface of base of claw. Branch to digit IV becomes enclosed within tendon of *M. flexor perforatus digiti* IV but soon perforates that tendon, sends elastic branches to distal ends of phalanges 2, 3, and 4, and finally inserts on ventral surface of base of claw.

Action. Simultaneous flexion and adduction of digits II, III, and IV and extension of tarsus.

Comparisons. In the Gruidae the belly in _Grus_ occupies only the proximal third of the tibiotarsus, but in _Balearica_ (and _Aramus_) it extends along the whole proximal half. In _Grus_ the tendon passes through a separate bony hypotarsal canal. In _Balearica_ this canal is not quite closed (in _Aramus_ it is merely a deep groove). In _Grus_ a branch of the inserting tendon extends to the hallux, but this is probably the same as the branch of _M. flexor hallucis longus_ extending to this digit in _Balearica_ (and _Aramus_). In _Grus_ a small elastic tendon, lacking in _Balearica_ (and _Aramus_), passes to phalanx 1 from the branch of the tendon to digit II. In _Balearica_ (and _Aramus_) a similar elastic tendon passing to phalanx 2 of digit IV is present, but is absent in _Grus_.

In the Rallidae the belly is similar to that of _Aramus_, but minor differences are found in the inserting tendon. Ossification of the tendon in both rallids occurs only along the tarsus (on the tibiotarsus as well in _Aramus_). The connection to the tendon of _M. flexor hallucis longus_ occurs farther proximally than in _Aramus_. All the small elastic tendons found in _Aramus_ are present in both rallids, but in _Rallus_ an additional one passes to phalanx 1 of digit III, and in _Fulica_ there are two passing to phalanx 2 of digit II (only one to this phalanx in _Aramus_).

Summary. The length of the belly is less in _Grus_ than in _Balearica_ or the non-gruids. The inserting tendon is ossified along both the tibiotarsus and the tarsometatarsus in _Aramus_ and Gruidae, but only along the tarsometatarsus in

Rallidae. The small, elastic tendons are similar in *Aramus* and *Balearica* but differ slightly in *Grus* and the two rallids.

143. *M. peroneus brevis*

Very small and slender muscle with partly pinnate belly and medium-long inserting tendon. Belly located on anterior face of full length of fibula. Attaches to fibula and to tarsometatarsus.

Lies partly deep to *M. tibialis anterior* and partly deep to *M. peroneus longus*.

Origin. Arises fleshily from anterior face of full length of fibula.

Insertion. Ossified tendon forms within belly, passes distad and through separate fibrous loop in anterolateral edge of distal end of shaft of tibiotarsus, passes across side of external condyle, and inserts strongly onto small tubercle in center of proximal face of hypotarsus.

Action. Probably extends tarsus.

Comparisons. In the Gruidae the belly in *Balearica* (and *Aramus*) extends the full length of the fibula, but in *Grus* it extends only from the insertion of *M. extensor ilio-fibularis* to the end of the middle third of the fibula.

In the Rallidae the muscle in both rallids is longer distally and wider than in *Aramus*, but in *Fulica* it is by far widest and thickest. In both rallids the inserting tendon is wider than in *Aramus*.

Summary. The muscle is similar in all, except for the length of the belly. In *Grus* it is quite short, in *Aramus*

and *Balearica* it is of intermediate length, and in the Rallidae, especially in *Fulica*, it is longest.

144. *M. extensor digitorum longus*

Medium-small muscle with elongately-triangular, flattened, and bipinnate belly; inserting tendon long and branched. Lies on anterolateral face of proximal half of tibiotarsus. Attaches to tibiotarsus and to digits II, III, and IV.

Lies entirely deep to *M. tibialis anterior* and *M. peroneus longus*. Separated from belly of *M. peroneus brevis* by narrow space along lateral edge.

Origin. Arises fleshily from elongate, triangular area involving most of lateral face of inner cnemial crest, base of anterior face of outer cnemial crest, and narrow area extending from between above two crests through proximal half of anterior face of shaft of tibiotarsus.

Insertion. Ossified tendon forms within belly and passes length of tibiotarsus, passes through bony bridge beneath tendon of *M. tibialis anterior*, through tendinous bridge on proximal end of tarsometatarsus, and extends along anterior face of tarsometatarsus. Four-fifths of way out tarsometatarsus tendon bifurcates, but branches remain connected by wide tendinous sheet. Lateral branch passes through lateral intertrochlear notch, where it merges with strong band of connective tissue running transversely across bases of digits. Tendon bifurcates at this point and one branch passes out dorsal surface of digit IV, becomes wider and somewhat

dissected, and attaches mainly to distal ends of first three phalanges and onto base of claw. Medial branch passes out dorsolateral edge of digit III, merges with tendon from medial branch of main tendon, and inserts broadly on distal ends of phalanges 1 and 2 and on base of claw. Medial branch of main tendon becomes wide in region over trochleae and bifurcates. One branch passes out dorsolateral edge of digit II, widens, and inserts on distal end of phalanx 1 and on base of claw. Other branch passes out digit III, merging and inserting with tendon of the same muscle previously described on this digit.

Action. Extends digits II, III, and IV and flexes tarsus.

Comparisons. In the Gruidae the belly of this muscle is usually shorter than in *Aramus*. In *Grus*, but not in *Balearica* (or *Aramus*), a portion of the origin is from *M. tibialis anterior*. In *Balearica* (and *Aramus*) a small branch from each of the two major branches of the inserting tendon passes to digit III. In *Grus* a single branch passes to this digit.

In the Rallidae the belly extends slightly beyond the proximal half of the shank (ends at middle of shank in *Aramus*). In *Fulica* (and *Aramus*) the inserting tendon is well ossified on both shank and tarsus, but in *Rallus* ossification is entirely absent. In the two rallids the pattern of the inserting tendons is similar to that of *Aramus*, but the branches are connected by stronger sheets (connecting sheets are thin and weak in *Aramus*).

Summary. The length of the belly is least in Gruidae, intermediate in *Aramus*, and greatest in Rallidae. In *Grus* a single branch of the inserting tendon goes to digit III, but in *Balearica* and the non-gruids a double branch passes to this digit. Ossification of the inserting tendon is lacking only in *Rallus*. The branches of the inserting tendon are more strongly connected in Rallidae than in the non-rallids.

145. *M. popliteus*

Very small muscle composed of short fibers; belly divisible into superficial and deep portions. Lies across proximal portions of posterior faces of tibiotarsus and fibula. Attaches to fibula and to tibiotarsus.

Fibular end of belly deep to *M. flexor digitorum longus*, and remainder deep to portion of *M. flexor hallucis longus*. Posterior edge contacts belly of *M. plantaris*.

Origin. Arises mainly fleshily from small area on posteromedial corner of proximal end of fibula.

Insertion. Attaches by fleshy and tendinous fibers to small area of posterior face of tibiotarsus, just proximal to origin of *M. flexor digitorum longus*.

Action. May pull head of fibula posteromediad or may merely hold it in position.

Comparisons. In the Gruidae the muscle differs from that of *Aramus* in lacking the division, but otherwise the muscle is similar to that of *Aramus*.

In the Rallidae the muscle is slightly larger than in *Aramus*, and no division is apparent (present in *Aramus*) in the belly.

Summary. This muscle is rather constant in all three families, although in the Rallidae it is slightly larger. In *Aramus* only, is there a good separation in the belly.

146. *M. plantaris*

Very small muscle with slender and somewhat pinnate belly and medium-long inserting tendon. Belly lies along upper third of tibiotarsus, deep within posteromedial portion of shank. Attaches to tibiotarsus and to tibial cartilage.

Lies medial to *M. flexor hallucis longus* and lateral to medial head of *M. gastrocnemius*. Lies somewhat superficial to belly of *M. flexor digitorum longus*.

Origin. Arises fleshily from narrow area on posterior edge of tibiotarsus, adjoining medial edge of insertion of *M. popliteus* and of proximal portion of origin of *M. flexor digitorum longus*.

Insertion. Slender, ossified tendon forms within belly and continues distad to insert on medial region of proximal edge of tibial cartilage.

Action. Braces and retracts tibial cartilage.

Comparisons. In the Gruidae this muscle is essentially the same as in *Aramus*.

In the Rallidae the belly of the muscle is longer and thicker in *Fulica* than in *Rallus* (or *Aramus*). Only a slight degree of ossification is present in the tendon in the two rallids (well ossified in *Aramus*).

<u>Summary</u>. This muscle has only very minor variations among the three families. The belly is slightly larger in <u>Fulica</u> than in <u>Rallus</u> and the non-rallids. The inserting tendon is well ossified in <u>Aramus</u> and the Gruidae but is very poorly ossified in Rallidae.

147. <u>M. extensor hallucis longus</u>

Very elonagte but poorly developed muscle. Located on anterior face of tarsometatarsus and partly on anteromedial face.

Proximal and somewhat superficial to <u>M. abductor digiti</u> II. Fused along medial edge with <u>M. extensor brevis digiti</u> IV.

<u>Origin</u>. Arises by few fleshy bundles from medial portion of inner extensor groove on proximal two-thirds of tarsometatarsus and from anteromedial edge of distal third of same bone. Bundles along lateral edge in common with <u>M. extensor brevis digiti</u> IV.

<u>Insertion</u>. Fleshy bundles attach to very slender, ossified tendon that passes full length of belly, out onto medial edge of digit I, and inserts on fascia over proximal phalanx.

<u>Action</u>. Extends digit I.

<u>Comparisons</u>. In the Gruidae the insertion in <u>Balearica</u> and <u>G. americana</u> is on the base of phalanx 1, but in <u>G. canadensis</u> it is on the distal phalanx (in <u>Aramus</u> it is on fascia enclosing the hallux).

In the Rallidae the muscle is similar to that of Aramus, except that the insertion is on the distal phalanx (on fascia in Aramus).

Summary. The muscle is constant among the genera studied, except for slight variations in the insertion.

148. M. extensor proprius digiti III
M. extensor brevis digiti III

No fleshy fibers are found for either of these muscles, and the only representative seems to be a tiny tendon arising from a minute area, just lateral to the more lateral insertion of M. tibialis anterior, and passing distad onto the base of digit III.

Comparisons. In the Gruidae the two muscles are similarly reduced. No fleshy components are found in Balearica, but a few occur proximally in G. americana and a few distally in G. canadensis.

In the Rallidae a very small, but well defined, fleshy belly occurs at metatarsal III in both rallids.

Summary. This muscle is extremely reduced in all the genera studied. A small, well defined belly remains at the distal end in the Rallidae only.

149. M. extensor brevis digiti IV.

Poorly developed muscle with flat, elongate belly composed of short, bipinnately arranged bundles. Located on anterolateral face of tarsometatarsus. Attaches to tarsometatarsus, to M. extensor hallucis longus, and to digit IV.

Lies partly deep to tendons of _M_. _extensor_ _digitorum_ _longus_ and _M_. _extensor_ _brevis_ _digiti_ III. Lies along lateral edge of and partly in common with _M_. _extensor_ _hallucis_ _longus_.

Origin. Arises from lateral region of extensor groove on anterior face of tarsometatarsus. Extends from insertion of _M_. _tibialis_ _anterior_ to external intertrochlear notch. Bundles along medial edge in common with _M_. _extensor_ _hallucis_ _longus_.

Insertion. Small, ossified tendon runs nearly full length of belly and, at distal end, passes through distal foramen to insert on medial side of proximal edge of phalanx 1 of digit IV.

Action. Adducts digit IV (see Fisher, 1946).

Comparisons. In the Gruidae the belly is quite reduced in its proximal third (in _Aramus_ this portion is thinner, but still well developed). In _Balearica_ (and _Aramus_) the belly arises in common with _M_. _extensor_ _hallucis_ _longus_, but this condition is not mentioned for _Grus_.

In the Rallidae the proximal third of the belly in _Rallus_ is more reduced than in _Fulica_ (or _Aramus_). In _Fulica_ the belly is considerably larger than in _Rallus_ (or _Aramus_).

Summary. This muscle is quite reduced in all three families, and the proximal end is greatly reduced in Gruidae and _Rallus_, The muscle is by far best developed in _Fulica_.

150. *M. abductor digiti* II

Small muscle with flat, triangular belly. Located on medial face of distal end of tarsometatarsus. Attaches to tarsometatarsus and to digit II.

Lies anterior to belly of *M. flexor hallucis brevis* and lies medial to *M. extensor brevis digiti* III.

Origin. Arises fleshily from medial face of distal one-sixth of tarsometatarsus.

Insertion. Tendon forms at distal end of belly and extends distad to insert along medial face of full length of phalanx 1 of digit II.

Summary. This muscle in Gruidae and Rallidae inserts on the base of phalanx 1, but in *Aramus* the tendon inserts on the full length of that phalanx. Other features are similar among the three families.

151. *M. flexor hallucis brevis*

Small muscle composed of two separate parts. Proximal part triangular, flat and bipinnate; distal part smaller and also triangular. Located on posteromedial side of tarsus. Attaches to tarsometatarsus and to digit I.

Proximal part lies medial to *M. adductor digiti* II. Distal part lies partially deep to tendon of *M. flexor hallucis longus* and adjoins posterior edge of *M. adductor digiti* II.

Origin. Proximal part arises fleshily from proximal end of tarsometatarsus, from triangular area involving medial face of hypotarsus as well as from portion of extensor groove on posterior face of shaft. Distal part originates fleshily

from small area on posteromedial face of distal end of tarsometatarsus, just proximal to facet for digit I.

Insertion. Tendon of proximal part leaves distal end of belly about one-fourth way out tarsus and passes distad to insert on lateral edge of base of phalanx 1 of digit I. Tendon is perforated at insertion by tendon of M. flexor hallucis longus. Very short tendon of distal part passes from distal end of belly and inserts on posterior face of base of phalanx 1 of digit I.

Action. Adducts and flexes hallux.

Comparisons. In the Gruidae the muscle in Balearica (and Aramus) is comprised of two separate parts, but in Grus apparently there is no division. In G. americana (and Aramus), but not G. canadensis or Balearica, the muscle is perforated by the tendon of M. flexor hallucis longus.

In the Rallidae the muscle is composed of two parts (as in Aramus). In Rallus the origin of the proximal part extends half-way down the tarsometatarsus, and in Fulica it extends the full length of the tarsometatarsus (in Aramus this origin extends through only the proximal fourth).

Summary. The muscle is apparently undivided in Grus, but it is composed of two separate parts with separate insertions in Balearica and the non-gruids. The extent of the origin of the proximal part is variable, but it is longest in Fulica, next in Rallus, lesser in Aramus, and is least in Balearica.

152. *M. adductor digiti* II

Very small and very slender muscle with medium-long inserting tendon. Located on posterior face of tarsometatarsus. Attaches to tarsometatarsus, to digit I, and sometimes to digits II and IV.

Lies deep to tendons of several toe flexors. Lies lateral to proximal part of *M. flexor hallucis brevis* and medial to *M. abductor digiti* IV.

Origin. Arises fleshily from lateral aspect of distal end of hypotarsus.

Insertion. Muscle becomes entirely tendinous in second fourth of tarsus. Tendon extends distad and usually inserts directly on anterior portion of base of phalanx 1 of digit I. Sometimes tendon may branch to insert weakly on digit II or digit IV as well.

Action. Flexes digit I.

Comparisons. In the Gruidae the muscle in *Balearica* has few if any fleshy fibers, but in *Grus* (and *Aramus*) there is a small fleshy belly. In *Balearica* the tendon branches to insert weakly on digits I and IV, but in *Grus* it inserts without branching on digit II (in *Aramus* the main insertion is on digit I, but it may also branch to digits II and IV).

In the Rallidae the belly is small, but well developed. extending about halfway down the tarsometatarsus (in *Aramus* it extends for less than one-fourth of the tarsus). In both rallids the single insertion is on the base of digit I (in *Aramus* this is the main insertion, but others may be present as well).

Summary. The development of the belly of the muscle is greatest in Rallidae and least in _Balearica._ The main insertion in _Aramus_ and _Balearica_, corresponding to the sole insertion in Rallidae, is on digit I, but in _Grus_ the insertion is on digit II. These variations indicate flexion of a different toe in _Grus_.

153. _M_. _lumbricalis_

This muscle is not visible in _Aramus_.

Comparisons. In the Gruidae the muscle is apparently absent in _Balearica_ (as in _Aramus_), but it is sometimes found in _G_. _canadensis_. See Berger (1956a) for a description. The muscle is not mentioned for _G_. _americana_.

In the Rallidae some apparently fleshy fibers occur on the tendon of _M_. _flexor_ _digitorum_ _longus_ in _Rallus_, but these can not be identified with certainty as belonging to the present muscle.

Summary. The muscle is either greatly reduced or absent in the genera studied, except in some specimens of _G_. _canadensis_, in which it consists of a few scattered bundles.

154. _M_. _abductor_ _digiti_ IV

Small, very elongate muscle with pinnate belly composed of very short bundles; belly very small in middle half of tarsus, larger at either end. Located near lateral edge of posterior face of tarsus. Attaches to tarsometatarsus, to _M_. _adductor_ _digiti_ IV, and to digit IV.

Lies deep to some of flexor tendons in tarsus. Located just lateral to _M_. _adductor_ _digiti_ II.

Origin. Arises fleshily and tendinously from posterior face of tarsometatarsus. Area of origin begins just lateral to hypotarsus and extends distad along lateral portion of posterior metatarsal groove approximately to level of distal foramen. Attached along distal portion of medial edge of belly of M. adductor digiti IV.

Insertion. Ossified tendon forms within belly, just distal to hypotarsus, and short, fleshy bundles attach to it down full length of tarsus. Tendon becomes large and superficial along distal fourth of tarsus and finally inserts on lateral face of base of phalanx 1 of digit IV.

Action. Abducts digit IV.

Comparisons. In the Gruidae the fleshy fibers in Balearica (and Aramus) are continuous along the length of the tarsometatarsus, although they are very sparse in the middle half. In G. americana apparently no fleshy fibers are present in the middle half, and the belly is considered two-parted. In G. canadensis fleshy fibers are apparently present only along the proximal third of the tarsometatarsus.

In the Rallidae the distal portion of the belly is larger than in Aramus, and the proximal end of the belly begins at the distal edge of the hypotarsus (in Aramus this end extends farther proximad, arising from the shaft of the tarsometatarsus lateral to the hypotarsus).

Summary. There is some variation within the Gruidae in the development of the middle region of the belly. The distal region of the belly is lacking in G. canadensis only.

The rallids differ from Gruidae and _Aramus_ in having a larger distal region of the belly and in having the hypotarsal portion of the origin beginning farther distad.

155. _M. adductor digiti_ IV

Very small muscle with very elongate, bipinnate belly. Located on distal portion of posterior face of tarsometatarsus, deep to tendons in that area. Attaches to tarsometatarsus, to _M. abductor digiti_ IV, and to digit II.

Lies deep to flexor tendons. Lies just medial to _M. abductor digiti_ II.

Origin. Arises by fleshy and tendinous fibers from distal three-fifths of posterior face of tarsometatarsus, from narrow area lying just medial to center of shaft.

Insertion. Tendon forms along medial edge of distal end of belly and inserts on anteromedial edge of phalanx 1 of digit II.

Action. Adducts digit II.

Comparisons. In the Gruidae the muscle in _Balearica_ is similar to that of _Aramus_, but the belly is not quite so well developed. In _G. americana_ and _G. canadensis_ the muscle is apparently lacking, although Hudson (1937) states that it is apparently represented by a fibro-elastic ligament in _Grus_.

In the Rallidae the muscle is better developed than in _Aramus_. It is larger in _Fulica_, extending proximad to the hypotarsus, but in _Rallus_ (and _Aramus_) it occupies the distal three-fifths of the tarsometatarsus.

Summary. The muscle is lacking, or at least is without fleshy components, in *Grus* but is present in *Balearica*. It is also present in *Aramus* and Rallidae. The muscle is best developed in the rallids, especially in *Fulica*.

DISCUSSION

Although the basic pattern of the musculature is similar in each of the five genera studied, a particular muscle may differ considerably in detail among the genera. The variations of major importance include such points as the presence or absence of the whole muscle, as well as pronounced differences in location of attachments, division into parts or accessory slips, size of the belly, and function. Differences of minor importance include variations such as the extent of attachments and amount of fusion to other muscles.

In order to analyze the degree of resemblance between *Aramus* and each of the other two families, the muscles are subjectively evaluated on the basis of intergeneric similarities. Each muscle in the limpkin is assigned a numerical value considered to be equivalent to its relative similarity to cranes and rails. In making these intergeneric evaluations, a minor resemblance is assigned 1 point, and each major correlation is assigned 2 points. The points indicating similarities to the cranes are then totaled, as are those indicating relations to the rails. When the values are the same for both families, the muscle is considered as without phylogenetic meaning. When the values are unequal the smaller sum is subtracted from the larger, the

remainder indicating the degree of relationship to the family used as the minuend. On this basis, a muscle of Aramus that has a major point of similarity with Balearica and Grus, for example, and a point of minor resemblance to Rallus, would be evaluated as follows:

Balearica	Grus	Rallus	Fulica		
2	2	1	0	Affinity:	Gruidae, 3 points

Thus a given muscle of Aramus may be categorized on the basis of its phylogenetic affinities and the degree of its relationship evaluated.

For a given muscle there are sometimes greater differences between genera of a single family than between members of different families. For this reason any single muscle may not be as useful as evidence of relationships as the pattern shown by all the muscles.

Great differences in body size complicate comparisons of the sizes of the muscles among members of the three families. To eliminate this difficulty, the size of a muscle is interpreted in relation to associated skeletal structures, rather than on the basis of its absolute size. Thus the length of the belly of a certain muscle would be similar in rails and cranes if in both it extends halfway out the humerus. Comparative sizes interpreted on this basis, even between cranes and rails, indicate that differences in body size among the members of these three families do not influence proportions of muscles. Thus Aramus, although intermediate in size between cranes and rails, does not generally have muscles of intermediate proportions.

Some exceptions to the foregoing generalizations are found. The smaller species have fewer vertebrae than the larger ones, and these differences are reflected in similar differences in the comparative overall length as well as in the number of components of the highly divided axial muscles. Another slight but clearly indicated exception is that the muscles of Fulica are generally bulkier than in Rallus. A final exception is one of individual variation, for most of the long wing muscles in larger specimens of Rallus have relatively shorter bellies than in smaller specimens.

Anatomical features that have remained conservative during the evolution of a group have special implications in taxomomy, as do features that are quite plastic and subject to rapid adaptation.

During the course of evolution the different regions of the body seem to have been influenced in different ways, reflected in various degrees of constancy of the regional musculature. For this reason, some regions lend themselves well to the study of evolutionary trends, but other more conservative ones are of little value. General characteristics of the musculature are discussed below according to regions.

Muscles of the Skull

The region includes 21 muscles that are associated with the skull and jaws. Its musculature has a comparatively moderate variability, since three muscles are generally variable among the genera, and only one is highly variable. One muscle is strongly conservative. Over half (12 of 21) are

useful in comparisons among the three families, and nine are without significance.

Of the 12 skull muscles of taxonomic value, eight show definite similarity to the cranes. These muscles and their values are as follows:

1. M. dermo-temporalis, 5
4. M. splenius capitis, 2
8. M. rectus capitis superior, 2
10. M. flexor colli brevis, 1
11. M. flexor colli profundus, 3
12. M. adductor mandibulae externus superficialis, 2
13. M. adductor mandibulae externus profundus, 3
16. M. pseudotemporalis, 5

Total points of relationship to Gruidae, 23.

Only four muscles of the region are similar in Aramus and the rails, as follows:

5. M. splenius accessorius, 3
7. M. rectus capitis lateralis, 2
19. M. pterygoideus dorsalis, 1
20. M. protractor pterygoideus, 4

Total points of relationship to Rallidae, 10.

The whole region in Aramus is, therefore, more like that of the gruids than the rallids, since twice as many muscles have the former correlation. When the total of all the values showing rallid similarity is subtracted from the total of the values of gruid similarity, the remainder is 13, which further indicates the predominance of aramid-gruid resemblance. Balearica is the crane that shows closest similarity to Aramus.

The most striking of the variations on the muscles of the skull and jaws is in the location of the anterior origin of M. dermo-temporalis. It arises from the postorbital

process in the rails, but from the posterolateral edge of the cranium in the limpkin and the two cranes. From the appearance of the skulls, the same condition holds for two other gruids, Anthropoides paradisea and A. virgo. An origin similar to that of the rallids is described by Shufeldt (1890) for Corvus corax and by Coues (1903) for Accipiter nisus. Figure 2 shows the origin of the muscle from the side of the skull in Gallus, between the postorbital process and the occipital region (see also Chamberlain, 1943). Both gruid or rallid types could have been derived by migration of the origin from the intermediate location in the supposedly primitive Gallus.

Another highly important muscle is M. pseudotemporalis. Its origin is almost entirely from the wall of the orbit in the rallids, but a large portion comes from the temporal fossa in Aramus and the gruids. The muscle in Aramus could be considered as being somewhat intermediate between that of the other two families, since both portions of the origin are well developed. Again the rallid condition conforms to that of at least some of the passerines (Beecher, 1951a, 1951b, 1953; and Shufeldt, 1890) and is, therefore, probably the more generalized.

The most important muscle showing similarities to the rails is M. protractor pterygoideus. In Aramus this muscle is divided, with an extensive insertion as in the rails. In the cranes the muscle is undivided with a more restricted insertion. The small size of the muscle makes one question its significance.

The muscles of the region have only a few distinctive features. A single muscle, M. biventer cervicis, in Aramus, has a unique location of the belly, but this is apparently related to size differences in the neck. The tendons of the jaw muscles of the limpkin are generally more highly ossified than in the other two families. This specialization could conceivably insure proper direction of pull and leverage for the operation of the long, specialized bill.

Muscles of the Hyoid

The region in Aramus is comprised of 17 muscles, two pairs of which are fused, to make a total of 15. The muscles are associated with the tongue, hyoid apparatus, throat, and the trachea. The whole region is neither outstandingly variable nor conservative, although three particular muscles are highly variable among the genera and are apparently associated with pronounced functional differences. Less than half (six of 15) of the muscles have usefulness in comparisons on the familial level, and nine have no significance.

Half of the six muscles showing affinities are similar in the limpkin and the cranes. These muscles and their values are as follows:

24. M. geniohyoideus, 2
28. M. ceratoglossus, 1
31. M. thyroglossus, 4
32. M. thyrohyoideus (31 and 32 are fused and counted as one)

Total points of relationship to Gruidae, 7.

The other three useful muscles show similarity between the limpkin and the rallids, as follows:

22. M. constrictor colli, 2
23. M. intermandibularis, 2
27. M. dermoglossus, 4

Total points of relationship to Rallidae, 8.

The whole region in the limpkin, therefore, shows approximately equal resemblance to rails and cranes. However, nearly half the muscles in the region show more similarity between _Aramus_ and _Balearica_ than between _Aramus_ and _Grus_.

The only highly important muscle showing similarity to the cranes is the combined _M. thyroglossus_ and _M. thyrohyoideus_. In _Aramus_ and the cranes these two muscles are completely fused into one long muscle that has an accessory part, but in the rallids the two muscles are separate, _M. thyroglossus_ being much shorter than _M. thyrohyoideus_, and there is no accessory part. The likeness of the condition of the two muscles in the limpkin and the cranes and the distinctness from that of the rallids is well-marked.

Of the three muscles showing greater resemblance to the Rallidae, only _M. dermoglossus_ is of major importance. It is present in the cranes but absent in the limpkin and in both rallids. However, it is a very thin muscle in the cranes, and dermal muscles are sometimes very variable, even between two members of the same family (see _M. dermo-temporalis_). Furthermore, the presence or absence of a muscle is not necessarily a good indication of phylogenetic relationships. For example, _M. genioglossus_ is well developed in _Grus_ and _Fulica_ but completely lacking in _Balearica_ and _Rallus_. For the above reasons, the comparative features of _M. dermo-_

glossus are considered less important than those of M. thyroglossus and M. thyrohyoideus.

The combined M. thyroglossus and M. thyrohyoideus has, in Aramus, an insertion on the entoglossum. This attachment is distinct from that of the other two families and must be associated with more ability to move the tongue laterally.

Muscles of the Orbit

The 12 muscles of this region are associated with the eyeball and eyelids. The whole region is conservative, as is each individual muscle. The muscles are also very similar to the comparable ones in the raven (Shufeldt, 1890) and to those of birds in general (Coues, 1903).

Muscles of the Wing

The region is comprised of 50 muscles associated with the wing and pectoral girdle. Over half (28 of 50) are useful in the study of relationships, and 22 are without significance.

Nearly all (26) of the useful wing muscles show much similarity between Aramus and the Gruidae. These muscles and their values are as follows:

51. M. tensor patagii longus, 6
53. M. pectoralis, 8
55. M. sternocoracoideus, 2
57. M. latissimus dorsi, 4
58. M. cucullaris, axillary part, 2
62. M. deltoideus minor, 2
64. M. proscapulohumeralis (brevis), 4
67. M. serratus profundus, 4
68. M. serratus anterior, 2
69. M. subcoracoideus, 4
70. M. biceps, 2
71. M. deltoideus major, 2

72. M. triceps, 6
75. M. anconaeus coracoideus, 4
78. M. supinator brevis, 2
79. M. flexor metacarpi radialis, 2
84. M. extensor longus digiti III, 2
85. M. flexor digitorum profundus, 4
86. M. flexor digitorum sublimus, 6
87. M. flexor carpi ulnaris, 4
88. M. flexor carpi ulnaris brevis, 4
89. M. abudctor alae digiti II, 4
92. M. flexor brevis digiti IV, 2
94. M. flexor metacarpi brevis, 1
97. M. extensor brevis digiti II, 2
99. M. flexor digiti II, 2

Total points of relationship to Gruidae, 87.

Only two wing muscles in the limpkin are more similar in the rails than in the cranes. They are 63. M. subscapularis (includes M. proscapulohumeralis), with a value of 2, and 81. M. pronator longus, with a value of 4. The total points of relationship to Rallidae are 6.

The whole region, therefore, shows an extremely high degree of aramid-gruid similarity, compared to a very low aramid-rallid likeness. When the total of the values of rallid similarity is subtracted from the total value of gruid similarity, the remainder is 81. This is further indication of the great predominance of aramid-gruid resemblance in the wing. This correlation is shown nearly equally in each subregion of the appendage, since approximately half the muscles of the shoulder, upper arm, forearm, and hand have definite aramid-gruid similarities. Within the framework of relationship to the cranes, Aramus is much more like Balearica than like Grus.

Half the muscles showing agreement between Aramus and Gruidae are of major importance. The most outstanding

features of each are as follows: *M. tensor patagii longus*, divisions of the inserting tendon and manner of insertion; *M. pectoralis*, insertion and lack of a dermal component; *M. latissimus dorsi*, insertion; *M. proscapulohumeralis (brevis)*, size and insertion; *M. serratus profundus*, insertion; *M. subcoracoideus*, origin and insertion; *M. triceps*, size and attachments to humerus; *M. anconaeus coracoideus*, presence of the whole muscle; *M. flexor digitorum profundus*, length and thickness; *M. flexor digitorum sublimus*, location and attachments of inserting tendon; *M. flexor carpi ulnaris*, division of the belly; *M. flexor carpi ulnaris brevis*, size of the muscle and location of the inserting tendon; *M. abductor alae digiti* II, sizes of the bellies.

One of the muscles with good aramid-rallid agreement is of major importance. This is *M. pronator longus*, and the pertinent characteristics are in the length of the belly and the location of the insertion. One of the muscles with good correlation between *Aramus* and *Balearica*, *M. flexor metacarpi brevis*, is most important since it is present in *Aramus* and *Balearica* but absent in *Grus*. One muscle, *M. coracobrachialis posterior*, has a sternal attachment in *Aramus* only. This feature is not completely unique, however, for a similar attachment has been mentioned by Fisher (1946) for cathartid vultures.

Muscles of the Tail

The region is made up of 11 muscles that operate the tail. Only one of these is highly variable, and none are

conservative. All except one of the 11 muscles are useful in interfamilial comparisons.

Of the 10 useful muscles, eight have better agreement between _Aramus_ and the gruids as follows:

102. M. levator coccygis, 2
103. Mm. interspinales, 2
104. M. levator caudae, 2
106. M. depressor caudae, 6
107. M. levator cloacae, 2
108. M. depressor coccygis, 1
110. Mm. intercoccyges, 4
111. M. expansor rectricum, 1

Total points of relationship to Gruidae, 20.

Only two muscles show greater similarity between the limpkin and the rails. These are 105. _M. lateralis caudae_, with a value of 1, and 109. _M. lateralis coccygis_, with a value of 4. Total points of relationship to Rallidae are 5.

Therefore the whole region shows four times as many muscles with aramid-gruid similarity as those with aramid-rallid agreement. When the total value of rallid correlations is subtracted from the total value of gruid relationship, the remainder is 15. This is further indication of the predominance of aramid-gruid agreement. _Aramus_ has more muscles like those of _Balearica_ than like those of _Grus_.

Only two muscles with aramid-gruid resemblance are of major importance. One is _M. depressor caudae_, which has one part in non-rallids, two in Rallidae. The other is the series of _Mm. intercoccyges_, which are much reduced in _Aramus_ and the cranes, but are well developed in the rails. Of the group with aramid-rallid resemblance, _M. lateralis coccygis_ is of major importance on the basis of the number of fasciculi.

Unique aramid characteristics occur in three muscles in the region. These are M. adductor rectricum, which has a separate belly; M. depressor caudae, with an origin of intermediate condition; and M. lateralis coccygis, which has strong fusion to another muscle.

Muscles of the Leg

The 44 muscles of the pelvic appendage make up this region. Three of these are highly variable and one is generally variable. Only two muscles in the region are strongly conservative. Over half (29 of 44) have some importance in comparisons among the families, and 15 have no significance.

Over half (17) of the 29 useful muscles indicate similarity of the limpkin with the cranes. These muscles and their values are as follows:

112. M. extensor ilio-tibialis lateralis, 2
115. M. gluteus profundus, 2
118. M. vastus lateralis, 1
122. M. flexor cruris medialis, 3
123. M. caudofemoralis, 1
124. M. flexor ischiofemoralis, 5
129. M. "femoritibialis externus," 6
131. M. obturator internus, 2
133. M. gastrocnemius, 2
137. M. flexor perforans et perforatus digiti III, 4
138. M. flexor perforatus digiti IV, 4
139. M. flexor perforatus digiti III, 2
140. M. flexor perforatus digiti II, 4
141. M. flexor hallucis longus, 1
144. M. extensor digitormm longus, 1
148. M. extensor proprius digiti III, 2 (plus M. extensor brevis digiti III)
154. M. abductor digiti IV, 4

Total points of relationship to Gruidae, 46.

Aramus has 12 muscles that are more like those of Rallidae than those of Grus, but none of them are of major importance. They are as follows:

116. M. iliacus, 2
117. M. ilio-trochantericus medius, 1
121. M. flexor cruris lateralis, 2
125. M. adductor superficialis, 2
126. M. adductor profundus, 2
127. M. ambiens, 1
130. M. obturator externus, 1
135. M. tibialis anterior, 1
152. M. flexor digitorum longus, 1
151. M. flexor hallucis brevis, 1
152. M. adductor digiti II, 1
155. M. adductor digiti IV, 2

Total points of relationship to Rallidae, 17.

The whole region of Aramus, therefore, finds more similarity in the cranes than in the rallids, since five more muscles show the former correlation, and since the total value of aramid-gruid relationship is 29 points higher.

In the muscles of Aramus showing gruid agreement, five are of major importance, mainly in the following features: the origin of M. flexor ischiofemoralis; the size of the belly and the attachments of "M. femoritibialis externus", the length, thickness, and attachments of the belly of M. flexor perforans et perforatus digiti III; the width of the muscle and the points of attachment of M. flexor perforatus digiti IV; the number of heads of M. flexor perforatus digiti II, and the size of the belly and the position of the origin of M. abductor digiti IV.

Aramus has 15 muscles showing more similarity to Balearica than to Grus, but no muscles of the region in the limpkin are more similar in Grus than in Balearica. The most distinct feature of this group is the absence of the caudi-femoralis part of M. caudofemoralis in Aramus and Balearica, although this part is sometimes missing in Grus as well. Another of the

muscles, M. adductor digiti IV, is quite fleshy in the limpkin and the crowned crane (and Rallidae) but is absent, or at least without fleshiness, in Grus.

Some of the muscles have unique features in Aramus. M. flexor cruris medius has an additional origin and a separate pubic attachment in the limpkin, M. popliteus has a unique separation in the belly, and M. abductor digiti II has a specialized insertion. Most of the tendons of the leg muscles are highly ossified in Aramus. This condition is equally well-developed in the cranes but is much less evident in the rails.

Leg-muscle formulae have been used in the past to indicate phylogenetic relationships. The formulae for the genera used in the study show little more than the rather close relationship of the members of the three families. One significant point that is shown is the lack of formula-muscle A (caudi-femoralis part of M. caudofemoralis or of M. piriformis) in Aramus and Balearica, compared to its presence in Grus and the rallids. The leg-muscle formulae, as amended by Berger (1959), for the genera dissected are as follows:

	A	B	C	D	E	F	G	X	Y	Am	V	
Aramus	-	B	-	D	E	F	G	X	Y	Am	V	
Balearica	-	B	(?-)	D	E	F	G	X	Y	Am	V	
Grus	A	B	(+-)	D	E	F	G	X	Y	Am	V	(canadensis)
											-	(americana)
Rallus	A	B	-	D	E	F	G	X	Y	Am	V	
Fulica	A	B	-	D	E	F	G	X	Y	Am	V	

Code Letter	Name of Muscle
A	M. caudofemoralis (piriformis), caudi-femoralis part
B	M. caudofemoralis (piriformis), ilio-femoralis part
C	M. iliotrochantericus medius
D	M. piriformis (gluteus medius et minimus)
E	M. psoas (iliaeus)
F	M. plantaris
G	M. popliteus
X	M. flexor cruris lateralis (semitendinosus)
Y	M. flexor cruris lateralis (semitendinosus), accessory part
Am	M. ambiens
V	Vinculum between tendons of M. flexor perforatus digiti III and M. flexor perforans et perforatus digiti III

CONCLUSIONS

The overall similarity of the musculature of the three families is apparent, but many details vary. The patterns of overall occurrence of the different variations offer good evidence of phylogenetic affinities. No less than 100 muscles show affinities useful in interfamilial comparisons, but the remainder are without importance, either because of great variability or because of extreme conservatism. Of the muscles of phylogenetic importance, 11 show some generic variation, but the other 89 are largely constant at the family level.

In 73 muscles Aramus has closer similarity to Gruidae, and 27 muscles show closer resemblance to Rallidae. The combined value of the gruid group is 203, compared to the value of the rallid group at 50. Subtracting the rallid figure from the gruid figure gives a value of 153 and indicates a much greater resemblance to the cranes than to the rallids.

The similarity of pattern in Aramus and the cranes is also apparent in separate regions. In most regions there is a strong aramid-gruid similarity, both in numbers of muscles showing the relationship, as well as in the sum of the individual values. This relationship is by far most pronounced in the wing, where slightly over half the muscles show agree-

ment between _Aramus_ and the cranes. The leg also has a strong gruid similarity, although fewer muscles are concerned.

In two regions this relationship is not shown. The hyoid region in _Aramus_ has as many muscles showing similarity to cranes as to rails, but the combined value indicates a slight predominance of the latter. The orbit is so conservative that it is useless for showing either relationship.

This evidence strongly indicates that the overall somatic musculature of _Aramus_ has definitely closer phylogenetic affinities to the Gruidae than to the Rallidae. This similarity is best developed in the wing, although it is also pronounced in the leg and is apparent in other regions. Only the region of the hyoid does not conform, but the sifnificance here is extremely slight, if any. The orbital region is too conservative to be taxonomically useful.

Within the framework of similarity of _Aramus_ to the cranes, certain features of 51 of the muscles of _Balearica_ are almost identical with corresponding points in _Aramus_ and are quite distinctly different from conditions in _Grus_, although for many other features the two cranes are generally similar. Only seven muscles have characteristics that are similar in _Aramus_ and _Grus_ and different in _Balearica_. The regions that best exemplify the correlation are the leg, wing, hyoid, and skull. The same pattern is carried over into other features, notably the simple sternum and trachea of _Aramus_ and _Balearica_, compared to the pneumatic sternum and highly coiled trachea of _Grus_.

The evidence discussed above strongly indicates that Aramus is phylogenetically closer to Balearica than to Grus. Two possible evolutionary interpretations are that Aramus is a specialized offshoot of Balearica, or that both gruids arose from Aramus and that Balearica represents an intermediate between Aramus and Grus. Similarities of the limpkin to the rails are frequent enough to show that Aramus is probably phylogenetically closer to the rails than the cranes are to the rails. With this interpretation, it seems likely that the three represent separate evolutionary lines diverging from a common ancestral stock, from which Aramus is least removed.

The distinctive characters of Aramus do not allow that it be removed from its monotypic family, and the decidedly crane-like nature of Balearica prevents merger of the two in a common family. Furthermore, most features of the musculature are more alike in the two gruids than between Balearica and Aramus. However, if the presence of Aramus-Balearica similarities and the general absence of Aramus-Grus correlations does indicate relationships, it also indicates that certain features of the musculature are more conservative than the usual features used in taxonomy.

Intergeneric correlations are also found in some muscles. Certain features of a genus are similar in two or more genera of different families and different from the corresponding features in the other member of its own family. These groupings are various, but for the most part they concern minor points, and no general patterns are indicated by

them. Apparently these represent features retained from a common ancestor, or in some cases, convergence.

Certain features are unique in a certain genus. Those involving single muscles are mostly minor. A general specialization of *Aramus* is the high degree of ossification of tendons, usually as much as and often more than in the cranes, and invariably more than in the rails. This characteristic is most pronounced in the jaw musculature, where the ossifications may aid in maintaining proper directions of pull for proper leverage in operation of the long bill. Otherwise the specializations in the feeding habits of *Aramus* do not seem to be associated with significant modifications of the jaw musculature. One other outstanding example of specialization is found in the overall musculature of *Fulica*. Its muscles, especially dermal components and muscles of the leg, are proportionately bulkier than those in *Rallus* and the non-rallids. The dermal musculature is apparently related to the thicker feathering and the leg muscles to swimming specializations. Both evidently are adaptations to aquatic habitat.

The number of specimens dissected is too small to allow meaningful conclusions on individual variation. Fisher and Goodman (1955) found more frequent and more pronounced variation among their specimens of *Grus* than were found in this study, in a somewhat larger number of specimens of *Aramus*. In *Rallus* the lengths of the bellies of most of the long wing muscles varied inversely with the sizes of the specimens. These and the few other individual variations found in the study seem to be of little importance.

SUMMARY

The major skeletal muscles of the limpkin, _Aramus guarauna_, are compared with the musculature of selected members of the Gruidae and Rallidae. Comparisons of gruids are based on published descriptions of _Grus americana_ and _Grus canadensis_ and on original dissections of _Balearica pavonina_. Comparisons with rallids are based on dissections of _Rallus longirostris_ and _Fulica americana_.

Nearly all the muscles of these three related families are basically similar, but certain features of various muscles differ among the families. From these variations, conclusions may be drawn concerning interrelationships of the three families.

The various regions of the body are considered separately and each is evaluated as a unit. Predominant affinities of _Aramus_ and the gruids are shown in 73 muscles. This similarity is best developed in the wing, and to a lesser degree, in the leg.

Only 27 individual muscles show distinct _Aramus_-Rallidae affinities, and only one region illustrates an overall aramid-rallid relationship. This, the hyoid region, is more similar in _Aramus_ and Rallidae, but the resemblance is very weak. In another region, the orbit, the muscles are so conservative that no relationships are indicated by them.

Some points of specialization are noted. An outstanding one is the high degree of ossification in the tendons of the jaw in the limpkin. The large size of dermal muscles and muscles of the leg in _Fulica_ are also distinct from those of _Rallus_ and the non-rallids.

_M_. _expansor_ _rectricum_ is newly named in the study, as one of the caudal muscles. Other muscles that are discussed in the study, but are not mentioned by Fisher and Goodman for the whooping crane, are _M_. _expansor_ _secundariorum_ and _M_. _anconaeus_ _coracoideus_. These are described in other species by earlier authors.

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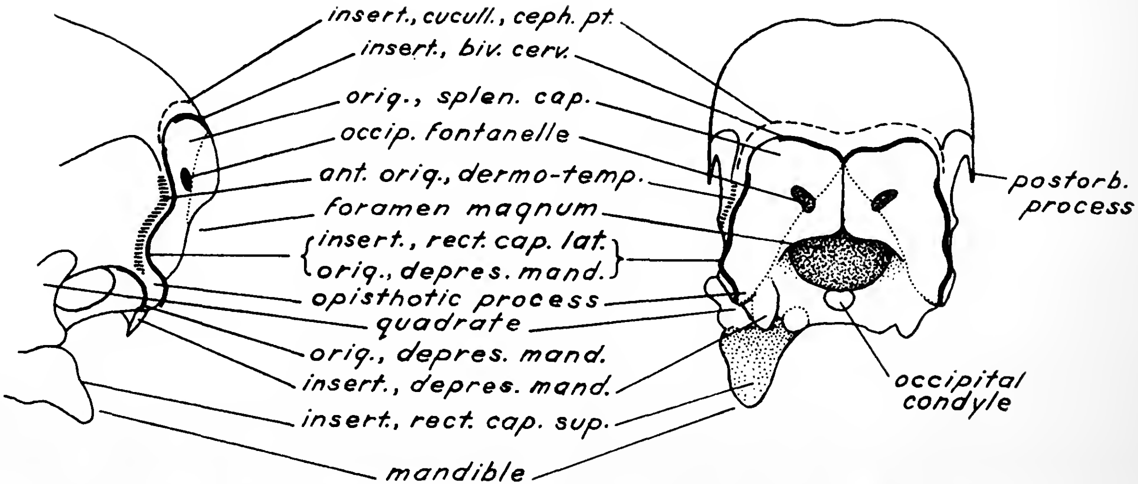

Figure 1.--Lateral and posterior views of the skull of the limpkin, showing attachments of the muscles in the occipital region.

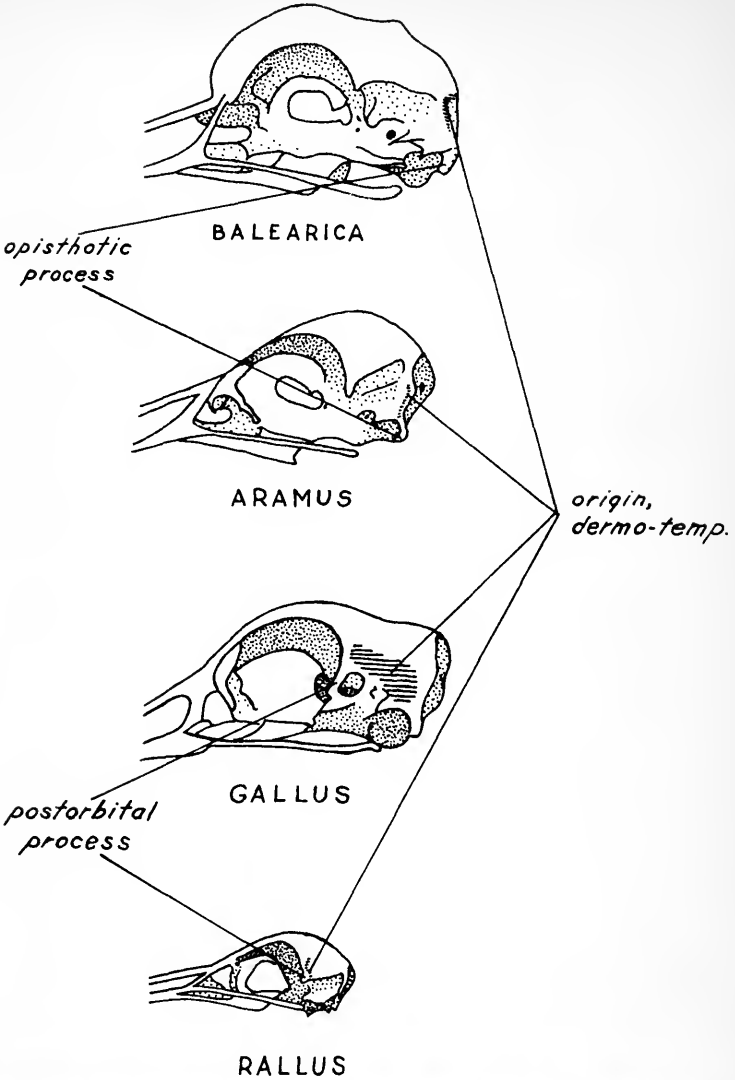

Figure 2.--Lateral views of the skulls of certain birds, showing the position of the cranial attachment (anterior origin) of M. Dermo-temporalis.

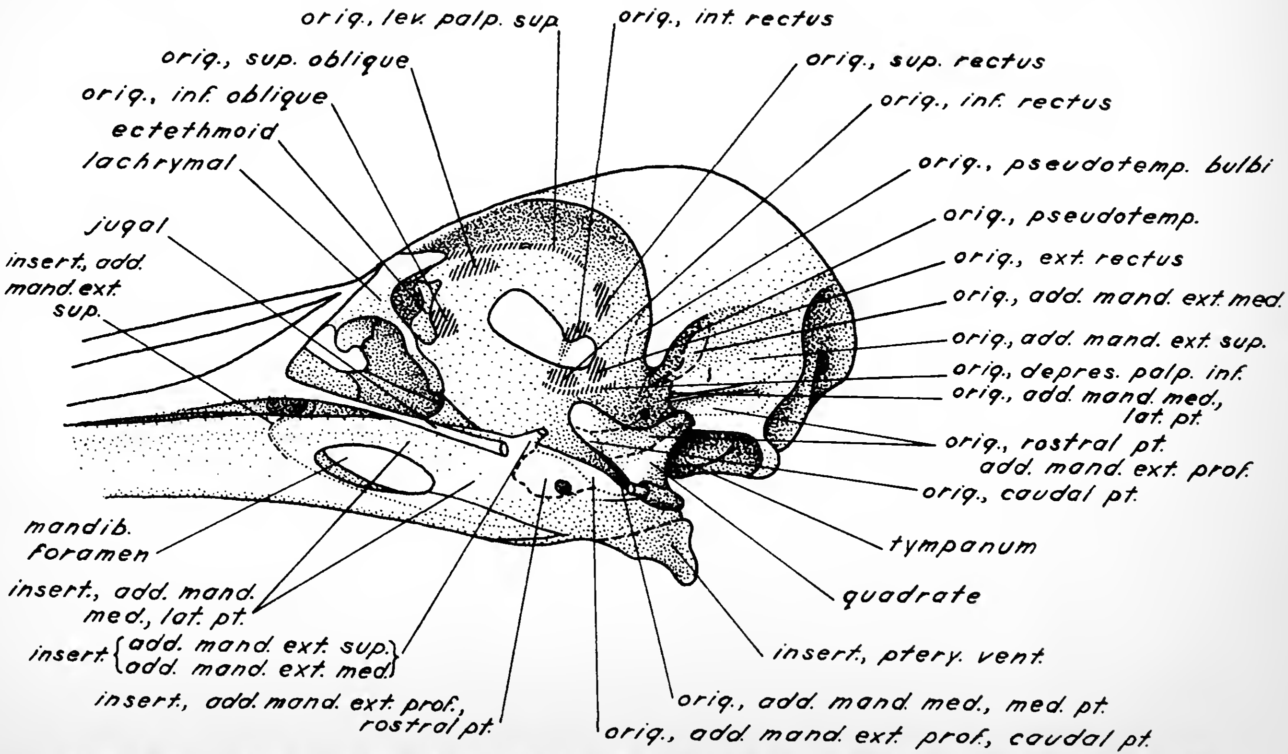

Figure 3.--Lateral view of the skull of the limpkin, showing attachments of the muscles of the jaws and of the orbit.

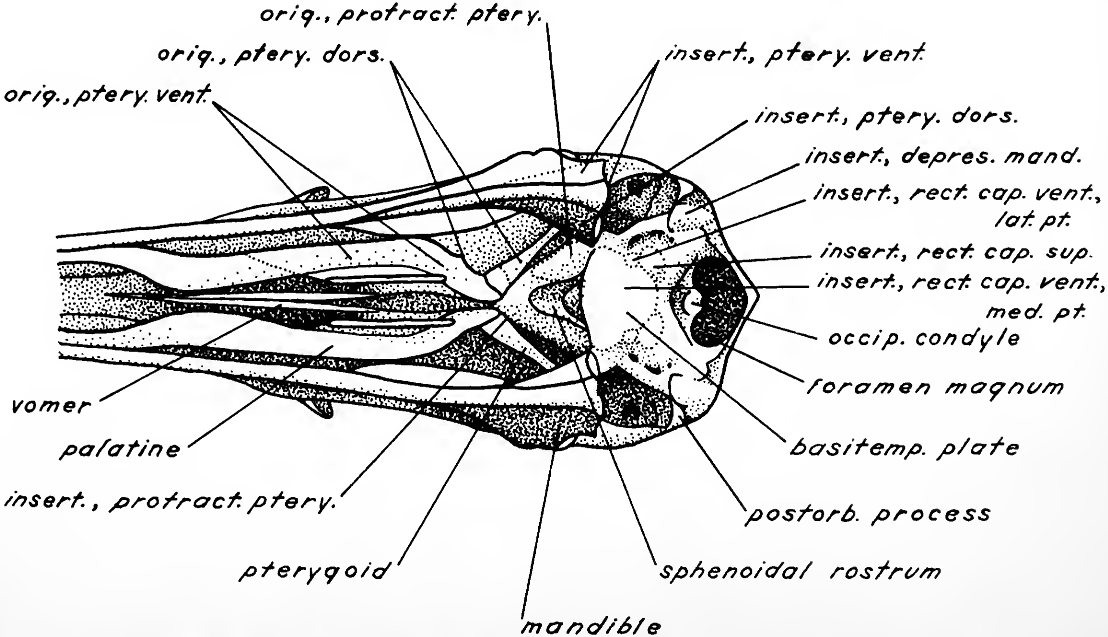

Figure 4.--Ventral view of the skull of the limpkin, showing attachments of muscles.

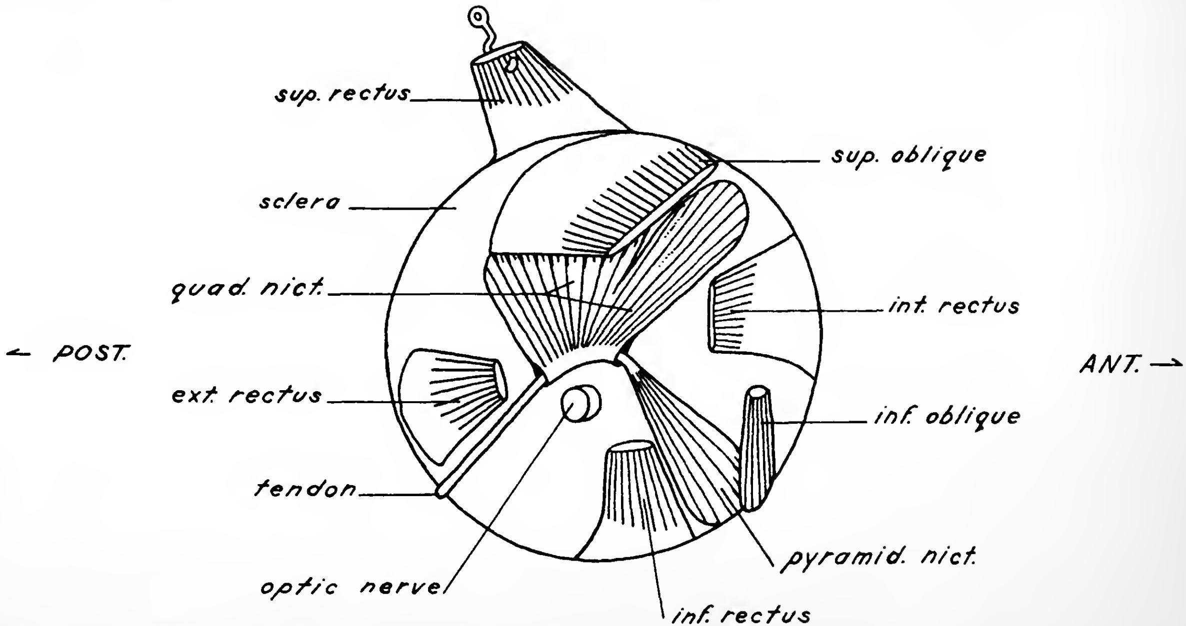

Figure 5.--Medial view of the left eyeball of the limpkin, showing the muscles of the eye and their attachments.

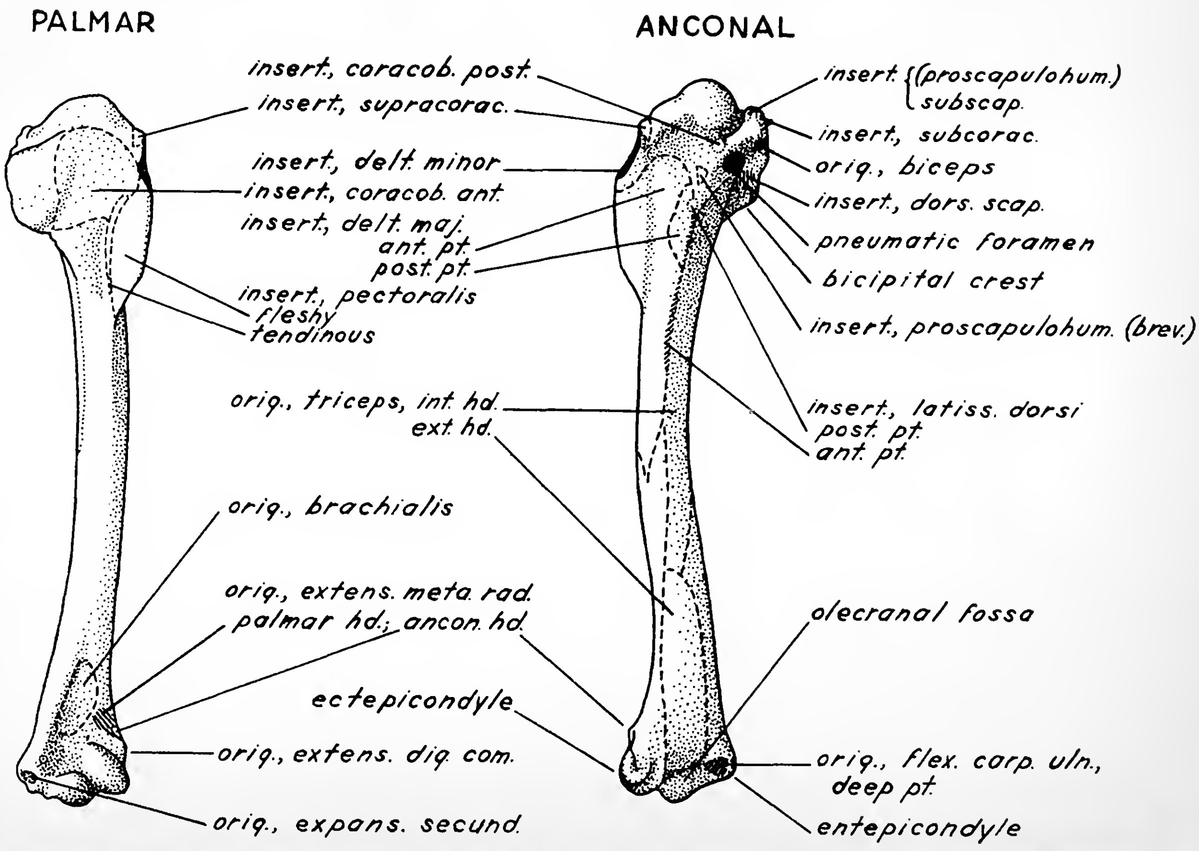

Figure 6.--Palmar and anconal views of the left humerus, showing attachments of certain muscles of the wing.

BIOGRAPHICAL SKETCH

The author was born in McKenzie, Tennessee, on March 22, 1932. His family soon moved to Florida, and he completed his early schooling in Miami. Undergraduate work was done at Murray State College at Murray, Kentucky, where he received the Bachelor of Arts degree with distinction in 1954. The next two years were spent in military service. Immediately following release from active duty, he spent two years at the University of Wisconsin as a graduate student and teaching assistant. He received the Master of Science degree in zoology from that institution in 1958.

Further graduate study was then begun at the University of Florida, where he held teaching assistantships as well as summer fellowships from the College of Arts and Sciences and from the National Science Foundation. In 1961 he accepted a full-time position as Instructor in Biological Sciences at Jacksonville University.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June, 1962

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